Starfish

A warning from the past regarding polarization in Science and Society

JOHN PATERSON

Starfish

Dr Peter James (left) and Dr Robert Endean (right) at Green Island

A warning from the past regarding polarization in Science and Society.

by

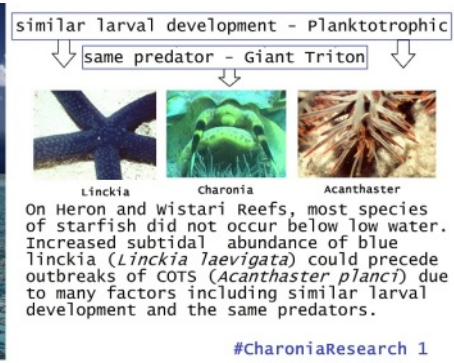
John Paterson

Contents

SUMMARY AND PRINCIPAL FINDINGS
SUMMARY OF RESEARCH
PREFACE
1985 INTRODUCTION
REVISED THESIS
CHAPTER 1. 1995 INTRODUCTION
CHAPTER 2. SPECIES PRESENT
CHAPTER 3. HABITAT
CHAPTER 4. POPULATION DENSITY
CHAPTER 5. SIZE STRUCTURE
CHAPTER 6. SEXUAL REPRODUCTION
CHAPTER 7. ASEXUAL REPRODUCTION
CHAPTER 8. CONSTANCY OF MEAN SIZE
CHAPTER 9. RELATIVE ABUNDANCE AND DIVERSITY
CHAPTER 10. GENERAL DISCUSSION
CHAPTER 11. REFERENCES
APPENDIX

SUMMARY AND PRINCIPAL FINDINGS

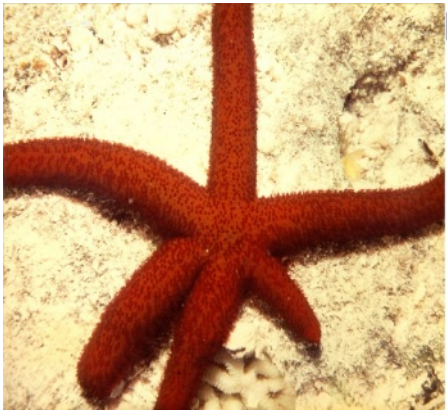
Increased sub-tidal abundance of blue linckia (Linckia laevigata) could precede outbreaks of COTS.

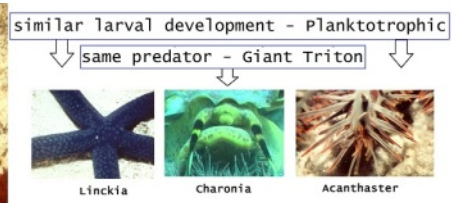

similar larval development - Planktotrophic
same predator - Giant Triton
Linckia
Charonia
Acanthaster
On Heron and Wistari Reefs, most species of starfish did not occur below low water. Increased subtidal abundance of blue linckia (Linckia laevigata) could precede outbreaks of COTS (Acanthaster planci) due to many factors including similar larval development and the same predators.
#CharoniaResearch 1

Most species of starfish are rare, cryptic, toxic and in one case (Acanthaster planci) even venomous.

similar larval development - Planktotrophic
same predator - Giant Triton
Linckia
Charonia
Acanthaster
On Heron and Wistari Reefs, most species of starfish are rare, cryptic, toxic and in one case even venomous
These two protected reefs are not known to have experienced COTS outbreaks even though outbreaks have been recorded further south on the GBR.
#CharoniaResearch 2

The preferred prey is the species hunted and attacked preferentially by the predator.



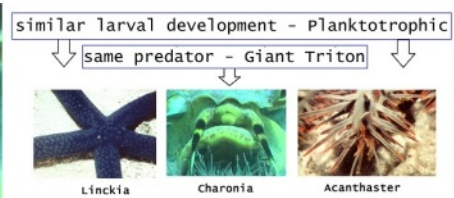

similar larval development - Planktotrophic
same predator - Giant Triton
Linckia
Charonia
Acanthaster
The preferred prey is the species that is hunted and attacked preferentially by the predator. Mortality data alone can not indicate a predator's preferred prey species as predatory attacks can be unsuccessful and predation can also be sub-lethal
#CharoniaResearch 3

Heron Reef (23° 27′ S, 151° 57′ E) in Capricorn Group at southern end of the Great Barrier Reef.

similar larval development - Planktotrophic
same predator - Giant Triton
Linckia
Charonia
Acanthaster
Heron Reef (23° 27' S, 151° 57' E) lies in the Capricorn Group which is towards the southern end of the Great Barrier Reef. It is a lagoonal platform reef with a vegetated cay at its western end. The cay supports a tourist resort and research station. A harbour has been dredged in the reef.
#CharoniaResearch 4

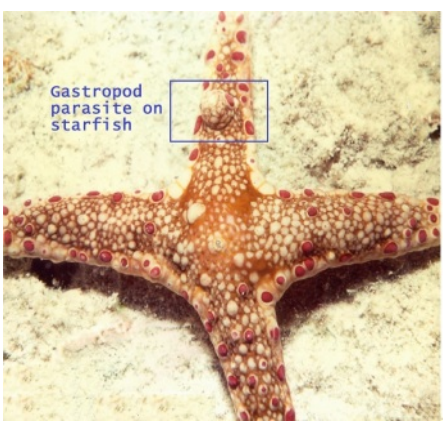
The attack of the triton elicits an escape response by the starfish.

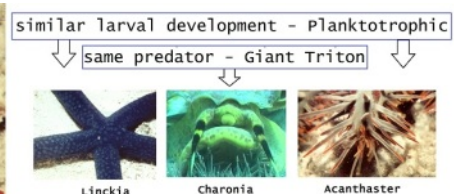
Starfish - Predator or Prey



The attack of the triton elicits an escape response by the starfish which, if successful, results in rapid prey dispersion with the loss of only a few arms. The escape response varies in its successfulness and is heavily dependent on (1) size and hunger of predator, (2) prey size and degree of cumulative prey injury and (3) physical composition and relief of substrate. #CharoniaResearch 5

Species of coral reef starfish may trigger larval settlement in the giant triton.

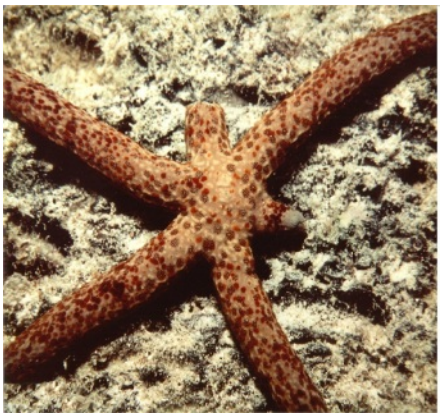


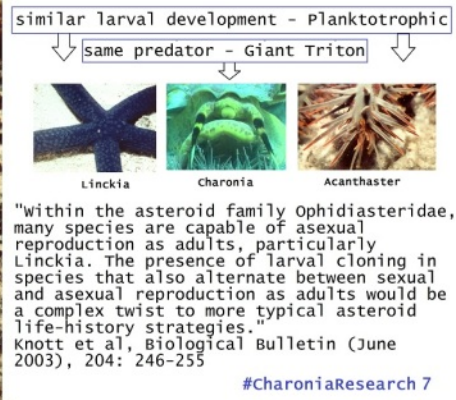


A number of species of coral reef starfish may trigger larval settlement in the triton. While previous studies managed to rear larva almost to the point of settlement, they could not produce settled larvae that crawled on the bottom. The cultured larva all died in the plankton and the missing link may well be another species of starfish.

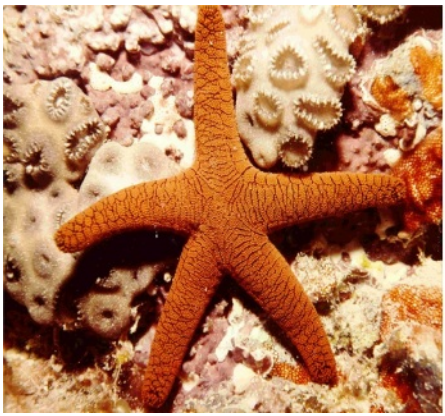
#CharoniaResearch 6

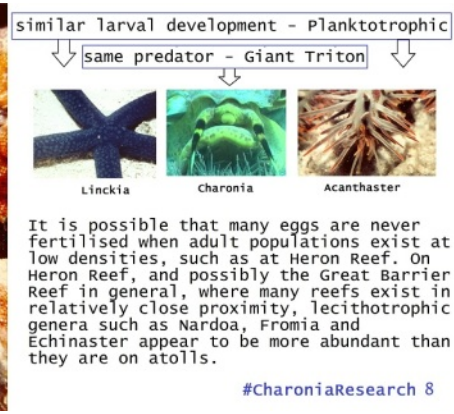
“a complex twist to more typical asteroid life-history strategies.” – Knott at al (2003)



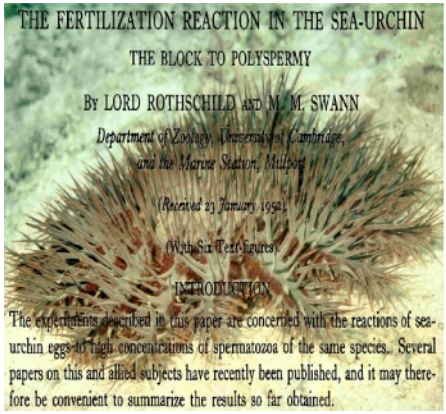

similar larval development - Planktotrophic
same predator - Giant Triton
Linckia
Charonia
Acanthaster
"Within the asteroid family Ophidiasteridae, many species are capable of asexual reproduction as adults, particularly Linckia. The presence of larval cloning in species that also alternate between sexual and asexual reproduction as adults would be a complex twist to more typical asteroid life-history strategies."
Knott et al, Biological Bulletin (June 2003), 204: 246-255
#CharoniaResearch 7

Many eggs may never be fertilised when adult populations exist at low densities.




similar larval development - Planktotrophic
same predator - Giant Triton
Linckia
Charonia
Acanthaster
It is possible that many eggs are never fertilised when adult populations exist at low densities, such as at Heron Reef. On Heron Reef, and possibly the Great Barrier Reef in general, where many reefs exist in relatively close proximity, lecithotrophic genera such as Nardoa, Fromia and Echinaster appear to be more abundant than they are on atolls.
#CharoniaResearch 8

Just like the fertilization reaction in the sea-urchin.



THE FERTILIZATION REACTION IN THE SEA-URCHIN

THE BLOCK TO POLYSPERMY

By LORD ROTHSCHILD and M. M. SWANN

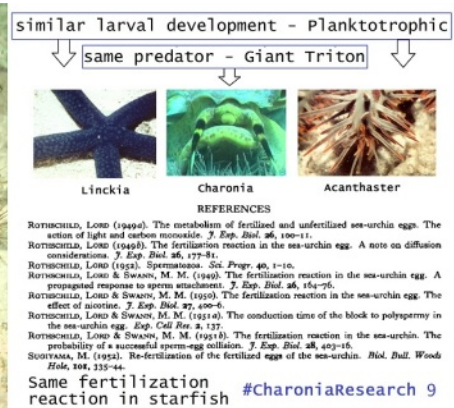
Department of Zoology, University of Cambridge, and the Marine Station, Millport

(Received 23 January 1952)

(With Six Text-figures)

INTRODUCTION

The experiments described in this paper are concerned with the reactions of sea-urchin eggs to high concentrations of spermatozoa of the same species. Several papers on this and allied subjects have recently been published, and it may therefore be convenient to summarize the results so far obtained.



REFERENCES

Rothschild, Lord (1949a). The metabolism of fertilized and unfertilized sea-urchin eggs. The action of light and carbon monoxide. *J. Exp. Biol.* **26**, 100–11.

Rothschild, Lord (1949b). The fertilization reaction in the sea-urchin egg. A note on diffusion considerations. *J. Exp. Biol.* **26**, 177–81.

Rothschild, Lord (1952). Spermatozoa. *Sci. Progr.* **40**, 1–10.

Rothschild, Lord & Swann, M. M. (1949). The fertilization reaction in the sea-urchin egg. A propagated response to sperm attachment. *J. Exp. Biol.* **26**, 164–76.

Rothschild, Lord & Swann, M. M. (1950). The fertilization reaction in the sea-urchin egg. The effect of nicotine. *J. Exp. Biol.* **27**, 490–6.

Rothschild, Lord & Swann, M. M. (1951a). The conduction time of the block to polyspermy in the sea-urchin egg. *Exp. Cell Res.* **2**, 137.

Rothschild, Lord & Swann, M. M. (1951b). The fertilization reaction in the sea-urchin. The probability of a successful sperm-egg collision. *J. Exp. Biol.* **28**, 403–16.

Sugiyama, M. (1952). Re-fertilization of the fertilized eggs of the sea-urchin. *Biol. Bull. Woods Hole*, **102**, 335–44.

Same fertilization reaction in starfish #CharoniaResearch 9

SUMMARY OF RESEARCH

Sea-urchins and starfish both belong to Phylum Echinodermata and while early research on the fertilization reaction was conducted by Rothschild and Swann (1949) on sea-urchins, the conclusions regarding egg fertilization and proximity of spawning individuals were just as applicable to starfish.

Human collection of the Giant Triton and other predators was suggested by Endean (1969) as a causative factor in starfish outbreaks, but this Predator Control Hypothesis was generally disregarded due to the enormous potential numbers of starfish. Recent research demonstrating the strong avoidance reaction of the starfish to the triton together with an understanding of the importance of starfish aggregation to reproductive success may be slowly changing this opinion.

The existence of crown-of-thorns starfish outbreaks influenced many important world economic decisions of the 1960s, including the rejection on ecological grounds of a new sea-level Panama Canal. Starfish radial nerve extract (1-methyladenine) has been used to experimentally induce starfish spawning since Noumura and Kanatani (1962), but any possible causal connection with the starfish outbreaks has never been investigated.

PREFACE

It's 1957 and Japanese scientists travel to the island of Miyake-Jima to study a strange disease affecting a coral reef. The island's people have noticed a strange increase in the number of the large, venomous crown-of-thorns starfish. Over the following years they kill large numbers of the starfish attempting to protect the living coral upon which the starfish is feeding. The Japanese scientists noted that they had observed giant triton shells feeding on the crown-of-thorns starfish, in research published only in Japanese.

5 years later

This same species of starfish is noticed in increasing numbers at Green Island, off Cairns here in Australia. Over the next five years, the starfish outbreak will consume much of the living coral at Green Island and other reefs in the vicinity.

The giant triton is again observed feeding on crown-of-thorns starfish and research in Queensland is commenced on the feeding rate and prey preference of the giant triton. Tests are done with three species of starfish; multiple specimens of each species are placed in cages with giant tritons.

The results showed that while each giant triton ate one crown-of-thorns starfish per week on average, it ate less crown-of-thorns starfish than another relatively common species of starfish. The research concluded that the crown-of-thorns starfish was not the preferred prey of the giant triton.

This conclusion was further supported by similar research done overseas, despite the observation that giant tritons were often located on the Great Barrier Reef, and elsewhere, were eating crown-of-thorns starfish.

30 years later

It becomes apparent that such a conclusion about prey preference of the giant triton is simply not justified, given the crown-of-thorns starfish often escapes complete predation because of its relatively high mobility. It is apparent that there is much confusion between prey capture and prey preference of the giant triton. It is suggested this distinction is relevant to control of prey.

40 years later

Australia is unsuccessful in its attempt to list the giant triton in Appendix 2 of the Convention in Trade in Endangered Species (CITES) because Japan objects on the grounds of ‘no evidence’ for the alleged endangered status of giant triton.

50 years later

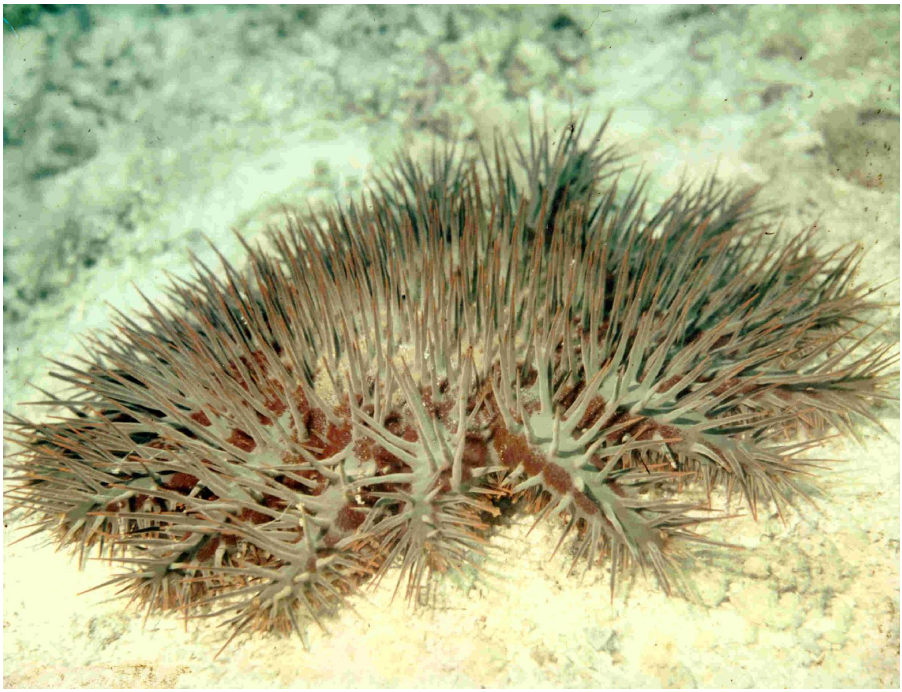
The Great Barrier Reef Marine Park Authority reports that outbreaks of crown-of-thorns starfish are a threat to the Great Barrier Reef and controls are needed.

60 years later

While the giant triton may be protected on the Great Barrier Reef and elsewhere in Queensland, there is still no evidence this protection has resulted in restored populations of the giant triton. However, there is evidence of continuing illegal collection and trade in Indonesia where it is also legally protected.

It is now worth reconsidering whether the existing local protection is sufficient or whether further international protection is required by listing the Giant Triton in Appendix 2 of the Convention on International Trade in Endangered Species (CITES).

The giant triton (Charonia tritonis) is a beautiful shell and a well-known predator of the crown-of-thorns starfish (Acanthaster planci). In many parts of the third world, it is still being collected in large numbers and sold to tourists as ornaments. As you admire the beautiful shell, spare a thought for the hungry mollusc that died. And don't forget, they live on starfish. Many species of starfish are known to outbreak in different parts of the world. Prior to human collection, the giant triton might have controlled starfish numbers not by eating the many, but by preventing the aggregation that precedes the outbreak. At present, little is known of any aspect of the triton's ecology despite its obvious importance in controlling starfish numbers.



1985 INTRODUCTION

The primary hindrance to any creative synthesis is the failure to recognize the causes of dissension in science. In some cases, a critic may doubt the integrity of either the scientist or the data. In these cases, further repetition of experiments may alleviate skepticism. In other cases, there may be a philosophical disagreement which has its basis in differing beliefs held by scientists.

These preconceptions, which all scientists possess can severely limit the process of conciliation. Dissension, however caused, is not easily resolved, and often leads to polarization within science. The failure of science to recognize and acknowledge explicitly, the validity of differing viewpoints based on the same data, demonstrates a confusion over these two causes of dissension.

Additionally, our aversion to implausible conjecture has limited the diversity of models which can be open to empiric testing. It must be remembered that, when seen through the eyes of a different culture, a model held to be true universally, may appear implausible. An example is our astonishment at the complexity of Micronesian fish-hooks which have been individually crafted to capture specific types of fish.

The pattern of relative planetary movements in our solar system was simplified greatly when the geo-centric model was discarded, in favor of a model in which the planets moved in orbits about the sun. These and other conceptual leaps have occurred when cultural limitations were waived temporarily, and the consequently greater insight justified the cultural changes which followed.

The phrase, "that is only conjecture", seems to imply that many

scientists regard conjecture as superfluous in the day to day running of science. In the pursuit of scientific rigor, we often overlook this necessary component of synthesis and find it increasingly difficult to model our thoughts in a manner which enables others to see a more distant horizon by standing on our shoulders.

Finally, the scientific process might not progress beyond the accumulation of facts. Often it appears impossible, from the data, to do more than simplify nature's variability by statistics, to categorize its variety by description or to model its behavior mathematically.

These techniques should be tools to further understanding of the interrelationships between the elements under study. To many workers the apparently stochastic nature of many phenomena prohibits a more detailed analysis.

In recent years there have been many studies in coral reef ecology, biology, and biogeography. Often, they are related, one to another, by a common principle or factor such as population outbreaks, plans for reef management or theoretical questions about the causes of diversity. Whenever several independent researchers study similar phenomena or ask similar questions, the possibility of dissension arises.

The ensuing debates, and even hostility, can appear as a failure in communication between the scientists concerned. More often the observed behavior results from philosophic disagreement taking its natural course. Philosophic changes in both science and society are often inseparable; they rarely occur, figuratively speaking, without bloodshed.

Philosophic clashes are likely to occur whenever the capacity to

acquire data, strategic to the opposing viewpoints, approaches a limit imposed by logistics or technology. This is certainly the case with much of the ecological debate over population outbreaks of crown-of-thorns starfish (COTS). The failure to recognize the symptoms of this fundamental disagreement can lead to much wasted effort, funds and, most of all, time.

Often, we need to determine which observations are required to swing general support from one model to another. However, the competing models may have reached the same level of logistic un-testability and there may be no logistically possible observation or series of experiments which could distinguish between the validities of either model.

There has been much debate about the relative roles of disturbance, stability, and niche specialization, as factors contributing to the co-existence of the large number of species in some communities. By contrast, there has been little consideration of the possibility that these factors and associated models may be of secondary importance to community order or structure itself.

The process of community succession follows a path of increasing complexity towards a hypothesized relatively static, climax community, the composition of which is determined by prevailing environmental as well as historical parameters. Throughout this process, as early (rapid) colonists are excluded by species that are competitively superior, the composition of the community changes.

The number of species present in the community increases to a maximum at some stage of succession, prior to the climax and subsequently decreases because of the exclusion of inferior competitors. The extent to which disturbance, by creating spatial and

temporal patches of early succession, acts to prevent the monopolization of available resources by a small number of superior competitors has been discussed extensively.

Other authors have either proposed or implied that high diversity communities are at equilibrium, and that species coexistence is mediated by the complex processes of interdependence and specialization that have evolved, in a physically benign environment, over long periods.

Additionally, the correspondence between stability in species composition and stage of community succession, is tautological because a successional climax is defined in terms of its temporal stability.

The progressive increase in diversity, biomass, complexity, and structure, resulting from the succession process, has been the focus of much discussion. In some instances, the co-existence of numerous species can be explained without resorting to complex, pattern oriented, models that require numerous assumptions which are testable only by prolonged, rigorous, and exacting field observation.

The almost universally accepted null hypothesis of "chance" does very little to enlighten biological scientists who want to understand or observe any existing inter-relationships between the species they study; that hypothesis, however, has gained a reverence totally unbecoming a statement that claims to say nothing at all.

Any function which may be played by community order or structure has, in the past, been so secondary to the aims or objectives of the "experimental approach", as to be uninteresting or considered logistically untestable (impractical or too difficult). However, there is a

fundamental difference between a model being logistically untestable and it being logically untestable. I do not propose that all the myths laid to rest by "Occam's Razor" be resurrected and considered as reasonable explanations of available evidence.

However, I do suggest that, in the field of coral reef ecology, our attempts to simplify the system under study have produced models that bear little relationship to reality. The rigid adherence to the least complex and ramifying hypothesis, has made it difficult to see beyond the generally accepted view of nature based on probability theory and chance.

While there have been many taxonomic and biogeographic works dealing with the coral reef starfish assemblage, the ecological requirements of starfish species occurring within the Indo-West Pacific region have not been studied extensively. It is known that many species occur on coral reefs throughout the region, while others possess a more restricted distribution. Several starfish species are known from only a few specimens and are rare.

The habitat requirements of coral reef starfish species, and the ecological roles of rare as well as of more common species are not understood. It is not known whether rarity is a survival strategy, an abundance limit imposed by predators or a failure in competitive ability of a species on its path to extinction. These questions have not been answered for this or any other taxonomic group within the highly diverse and complex ecosystem of the coral reef.

Competition and other ecological models and corollaries draw their scientific context often, by analogy, from the corresponding pattern of interaction observed within contemporary human society. The influence of one's cultural background in the initial perception and

subsequent acceptance of the ecological generality of these analogies is overlooked often.

A model is an abstraction only, but in common with all scientific models, socially analogous models can be raised, by consensus, to the status of paradigms, such that, observations which contradict the model are considered either inaccurate or implausible.

Assume that the population size of some organism is limited by the level of juvenile recruitment in such a way that the density of adults is never sufficiently high for one individual to interact significantly with another. If these assumptions were true but unknown, the interactions between adults and their ecological significance could be modeled incorrectly using competition theory.

Observations which are categorized within a severely limited body of theory cannot be regarded as empiric support for any hypothesis, as biased observations can provide support for any model.

It is possible that many organisms live presently at adult population densities which are sufficiently low to preclude both inter and intra-specific competition. In such species, the adult population density may be limited always, at some previous stage of the life cycle, and the adult populations may be free from density dependent interactions.

A range of reproductive strategies is found in coral reef starfish. Sexual recruitment can follow either planktotrophic or lecithotrophic larval development. The occurrence of parthenogenetic development, hermaphroditism or asexual reproduction may be correlated with survival at low population density and the consequential low probability of locating an opposite sexed conspecific at breeding time.

Within coral reef starfish, asexual reproduction has been observed in Linckia guildingii, Linckia multifora, Ophidiaster robillardi, Echinaster luzonicus and Asterina anomala. This provides evidence that, in some species under certain conditions, genetic variability and potential dispersal are less important to the maintenance of population numbers, than is continuity of recruitment.

The larvae of coral reef starfish generally require a solid substrate to complete their development, and a coralline algal substrate has been observed as the chosen settling surface for many species. More complex species-specific optima, located by sensitive chemo-sensory receptors might ensure settlement in habitats which are conducive to survival of post-settlement stages. Juvenile starfish have exponential growth during the period following settlement and are subject to high mortality during this period. The juveniles transform to adult morphology at a certain size and before this may look quite different from adults.

A general paucity of information about juveniles characterizes available data on population structures of large bodied, coral-reef starfish. It is possible that populations are maintained either by continual low recruitment or occasional high recruitment, each coupled with iteroparity.

The juveniles are cryptic, and their apparent absence or rarity indicates that reproductive success is either constantly low, sporadic or both. Sporadic success may depend on factors such as availability of planktonic food, level of planktonic predation or mortality of settled larvae. These may average out over the life-span of the adult resulting in stability of adult numbers. Population increases of coral reef starfish species have been well documented for COTS, and apparent population increases of Linckia laevigata following COTS outbreaks

have been described.

The differing requirements for growth and successful recruitment of juveniles, within the coral reef starfish assemblage, will have resulted in diverse life history strategies. A conceptual dichotomy exists in our perception of the life history of all organisms and is referred to as r- versus K- strategy.

These different survival characteristics are thought to have evolved in response to specific types of environments. The spectrum of existing life history attributes, apparent in any community study represents many points on a continuum between the conceptually ideal r-strategists and K- strategists.

If a population's size is limited mainly by competition, then natural selection will result in an increased competitive ability (K-selection) and, in populations which are not resource limited, selection will result in an increased reproductive rate (r-selection).

The reproductive effort (energy used for reproduction compared with the energy used for non-reproductive purposes) and age specific mortality schedule are an indication of the type of selection which has occurred during the evolution of a species.

The longevity of a species is determined by the relative probability of juvenile and adult survivorship. In the simplest case, if the probability of a sexually mature organism's survival from one reproductive season to the next is greater than the probability of one of the offspring reaching sexual maturity, then the species will exhibit iteroparity. The weighting of selective attributes is arbitrary (niche specialization, number and size of eggs, longevity, possession of toxin), as the absolute ends of the r-K continuum do not exist.

Unpredictable environmental factors (perils of larval life and enormous potential dispersion) can result in a high numerical fecundity, and consequentially, most marine benthic invertebrates have a high energy cost associated with reproduction.

The dispersal stage of a population spreads the risk of local extinction in space and time. The early stages of succession survive by being able to colonize regions quickly following disturbance. The resultant spatial and temporal variation in population size seems to characterize the typical r- strategists. Their populations are stable only when viewed on a larger scale. The spatial and temporal scale at which a species must be viewed for its numbers to be stable is an indication of its position on the r-K continuum.

The life history strategy, of each species, will be viewed in this context and a variety of strategies should be observed within the coral reef starfish assemblage. Early succession species would be expected to have large fluctuations while late succession species should have smaller ones. Stable, climax communities should be characterized by small fluctuations of their component species.

The apparent stability of any biological system is dependent on the scale of observation. At the organismic scale, there would be neither temporal nor spatial abundance variation if an individual exactly replaced itself, without dispersing, then died. At the population scale, a level of numerical stability, consistent with a model of community equilibrium and climax, could be achieved if dispersion, larval survival, and settlement phenomena did not result in greatly differing adult numbers from one year to the next.

Since the late 1950's, coral reefs of the Indo-West Pacific region have

experienced population outbreaks of the corallivorous crown-of-thorns starfish. The resultant loss of hard coral cover on some reefs of the Great Barrier Reef was studied during the period of outbreak, and subsequently, so that both the short- and long-term effects of this predator would be known.

The role of this predator in the elevation or lowering of coral species diversity on the Great Barrier Reef has not been studied adequately. It is apparent that some reefs become reinfested with starfish about 15 years following the initial infestation. It would appear, that when the quantity (not necessarily diversity) of a reef's hard coral cover has regrown, the starfish can recruit again in high numbers.

Although the COTS outbreak phenomenon has puzzled scientists for a quarter of a century, and although many explanatory hypotheses and models have been proposed, there remains disagreement about the causes of the phenomenon. Additionally, there is disagreement about the need for reef management strategies, that might mitigate the widespread effects of this coral predator.

The extent of present population outbreaks, and the possibility of past outbreaks (prior to 1960) have not been studied in sufficient detail to allow critical evaluation of either the problem itself, or the risks associated with incorrect management. We do not know what factors allow high recruitment of this starfish on some reefs when, on other reefs, it maintains a low population density.

The natural life expectancy, larval dispersal, and adult migration of this starfish, while central to an understanding of the phenomenon, are not understood sufficiently.

The role of natural predators in maintaining high diversity, and the

possible survival strategy of rarity in the coral reef community have not been studied adequately.

REVISED THESIS

For acknowledgements, data tables and figures refer to:

Paterson, John C. (1996). Persisters and opportunists in an assemblage of coral-reef starfish. PhD Thesis, School of Biological Sciences, The University of Queensland. https://doi.org/10.14264/uql.2014.567

CHAPTER 1. 1995 INTRODUCTION

Coral reefs seem to defy many of the paradigms which characterize less complex biological communities. While there is general agreement that the biota of coral reefs exhibit high species diversity, some authors have characterized coral reef assemblages by selecting species with high population densities (Sale, 1974; 1976; 1977; 1984; Sale and Dybdahl, 1975; Connell, 1978). Other authors have included rarer species (Kohn, 1959; 1968; Den Boer, 1971; Grassle, 1973) and Endean and Cameron (1990 a) have emphasized the importance of the role of these rarer species and stated that rarity is virtually ignored in most ecological models of the coral reef ecosystem. They suggest that our understanding of coral-reef ecology is influenced strongly by the constraints of many of the analytical tools being used in reef studies. As a result, they believe that most analyses have dealt primarily with species that are sufficiently numerous to provide statistically satisfactory numbers of records and that most studies have excluded rare species which, in fact comprise the majority of coral-reef species.

The complexity of coral reef ecosystems is not surprising given the great length of time that these ecosystems have been in existence. While the shallow water distribution of coral reefs has varied with the alternation of glacial and interglacial periods (Hays, Imbrie and Shackleton, 1976), in their broad biological form, coral reefs have existed since the Precambrian and reefs like present reefs have existed for around 50 million years (Newell, 1972). While stating that there is no general rule for coral-reef organisms, Endean and Cameron (1990 a) have suggested that the attribute of persistence possessed by most of the rarer species characterizes the majority of coral-reef species and is responsible for both structuring and perpetuating this ecosystem. They regard the coral reef ecosystem as being an ordered and predictable system. However, other authors (Sale, 1977; 1991; Connell,

1978) have different views.

Sale (1991) regards reef fish communities as open non-equilibrium systems with living space determined in a random manner. Connell (1978) regards intermediate levels of disturbance as essential to the maintenance of diversity in this and other highly diverse and complex ecosystems. There has been much discussion of the meaning of stability (MacArthur, 1955; Dunbar, 1960; Leigh, 1965; May, 1972; Jacobs, 1974; Margalef, 1974; Goodman, 1975; Peters, 1976; Pimm, 1984).

Endean and Cameron (1990 a) have put forward the hypothesis that complex, high diversity assemblages of coral-reef animals are characterized by a preponderance of rare but long-lived species that they have termed persisters. These persistent species exhibit low recruitment, low adult mortality and relative constancy of adult population numbers and population structure. They occur in association with opportunist species that have high recruitment, a high adult mortality and varying adult population numbers and population structure. While individuals belonging to opportunist species are more abundantly represented than those belonging to persistent species, Endean and Cameron believe that most species in the coral reef ecosystem are persistent species. This hypothesis has not been tested in the field.

As no general consensus relating to the organization of coral reefs has been reached in the literature, the persister / opportunist distinction is examined in this thesis, rather than a deep analysis of the opposing views relating to stability. Events that are stochastic and unpredictable at one spatial or temporal scale may be predictable at another. In addition, the stability or otherwise of any system may be determined, amongst other things, by the particular set of species that is chosen to

characterize the system.

The starfish fauna of coral reefs can be distinguished from the starfish fauna of surrounding waters (Endean, 1953; 1965) and coral-reef starfish may be regarded as an ecological entity. During studies of Queensland echinoderms, Endean (1953; 1957; 1961; 1965) found 18 species of starfish on Heron Reef. Although reference was made to the habitat, general abundance, and biogeography of each of the species, no detailed study of the Heron Reef starfish assemblage was made. This study will compare several ecological parameters in several species of starfish occurring on this coral reef. The population stability of the less abundantly represented, persistent species will be contrasted with that of the more abundantly represented opportunistic species. For the purposes of this study, the population stability of each species refers to the constancy of its population size structure over time.

Clark and Rowe (1971) and Yamaguchi (1975 b) reviewed the geographic distribution of many coral-reef starfish. Specimens of some species are frequently encountered and appear to be relatively common while others are known from very few specimens and appear to be extremely rare. The ecological requirements of coral-reef starfish, as well as the role of both rare and common species, are not understood and it is not known whether rarity is a survival strategy, an abundance limit imposed by predators or a failure in competitive ability of a species on its path to extinction. These problems have not been addressed for asteroids or any other taxonomic group within the highly diverse and complex coral reef ecosystem.

It has been suggested that longevity may characterize species of predictable environments (Frank, 1968; Grassle, 1973) or species with unpredictable pre-reproductive survival (Ebert, 1982; Goodman, 1974;

Murphy, 1968). Several authors (Frank, 1969; Grassle, 1973; Ebert, 1982) have found many coral-reef animals to be long lived and Endean and Cameron (1990 a) regard the long-term persistence of individuals at given sites as an ordering phenomenon in the coral reef ecosystem. Little information is available on the longevity of coral-reef starfish. Ebert (1983), Kenchington (1976), Cameron and Endean (1982) and Endean and Cameron (1990 b), believe that Acanthaster planci is a long-lived species, but Lucas (1984) suggested individual senescence in this species at an age of approximately five years. Stump and Lucas (1990) reported a linear growth pattern in aboral spine ossicles of this species which supported this suggestion, however the maximum age of this species has now been re-evaluated to at least 12-15 years (R. Stump, Ph.D. thesis). Yamaguchi and Lucas (1984) demonstrated a short-lived population structure in the small and cryptic starfish Ophidiaster granifer, but little is known of the longevity of other species of coral-reef starfish.

The severe effects of Acanthaster planci predation are well documented (Chesher, 1969 a, b; Endean, 1969) and the change in coral population structure following an A. planci population outbreak was reported by Cameron, Endean and Devantier (1991). Moran (1986) has compiled a bibliography on the Acanthaster planci population outbreak phenomenon. Research on temperate starfish species that undergo population outbreaks has been reviewed by Loosanoff (1961).

Little is known of the other coral-reef starfish species, and the reproductive patterns, population stability and diversity of starfish assemblages on reefs that have not carried population outbreaks of Acanthaster planci are poorly understood. Heron Reef is such a reef. It is a Marine National Park and is situated near the southern end of the Great Barrier Reef.

It should be appreciated that the number of species recorded in any study is determined by both the spatial and temporal scales of sampling as well as by the distribution and composition of the species in the assemblage (species richness or diversity). To allow some degree of standardization for collection effort, the rate at which the number of species in a sample increase with area of the sample (the species-area relationship) and the range of abundances within this assemblage (species relative abundance) have been chosen as a more representative measure of species richness than the total number of species. The species-area relationship, relative species abundance, and constancy of numbers and mean size (population stability) of coral-reef starfish are unknown elsewhere.

The fact that this study was undertaken on a reef that appeared to have low starfish abundance (and was not known to have carried an Acanthaster outbreak) generally precluded small-scale analyses that were dependent on high population densities. Large-scale traverse sampling is analogous to manta tows that have been used to monitor populations of Acanthaster. This scale of sampling is useful to establish a general pattern of starfish abundance but is not capable of providing detailed data on either microhabitat partitioning or small-scale abundance. It should provide a basis for future comparison with data from Heron and other reefs.

Sexual reproductive patterns have been studied in some of the coral-reef starfish species known to occur throughout the Indo-West Pacific. Most of these studies have been conducted on reefs that are known to have carried population outbreaks of Acanthaster planci (Yamaguchi, 1973 a, b; 1974; 1975 b; 1977 a; Yamaguchi and Lucas, 1984). In addition to providing reproductive data for these species from a reef that does not undergo such population outbreaks, this study will examine the reproductive patterns of previously unstudied species.

When the timing and extent of sexual reproduction along with the type of larval development exhibited by the various species studied are correlated, inferences can be drawn regarding the reproductive effort and dispersal capacity of each species involved. Endean and Cameron (1990 a) have suggested that opportunists and persisters are basically different with respect to their rates of recruitment, and a pattern should emerge when data on reproduction and population structure for several coral-reef starfish species are compared.

Several species of coral-reef starfish are known to exhibit asexual reproduction. The extent of asexual reproduction in the population maintenance of each species is an indication of the adaptive significance of this low-dispersal reproductive strategy. Many authors have commented on the role that may be played by this form of reproduction (Rideout, 1978; Yamaguchi, 1975 b; Ottesen and Lucas, 1982; Yamaguchi and Lucas, 1984) and Endean and Cameron (1990 a) have suggested that this mode of reproduction may assist species to withstand disturbance. Most species of starfish cannot reproduce asexually but are still capable of great powers of regeneration. Missing limbs in species that do not reproduce asexually may indicate sub-lethal predation.

Recruitment, migration, and mortality ultimately determine the spatial and temporal distributions of the starfish populations in the Heron Reef assemblage. There is a distinction to be drawn between reproduction and recruitment as well as between predation and mortality. Recruitment is a process that is complete only when an offspring reaches maturity and reproduces itself. Similarly, predation may only be sub-lethal and autotomized limbs may be regenerated or may become asexual recruits. Starfish mortality occurs only when all fragments of a starfish have died. For logistical reasons, it was decided not to examine potential predators in this study. Likewise, a detailed

examination of larval settlement processes was not undertaken. Migration of starfish is poorly understood as there is considerable difficulty in relocating tagged specimens particularly in autotomous species.

However, the interaction between the major determinants of population size mentioned above will influence the size-frequency distributions of each species. These distributions will be compared over time at Heron Reef and with size-frequency data from other localities. Mean individual size will vary with periods of recruitment and mortality, and size-frequency distributions that are constant over a study period of several years will suggest stability within the age structure. Alternately, such a finding could reflect the apparently static nature of a long-lived species when observed on a comparatively short time scale, even one of several years. However, study of the latter alternative could not be pursued beyond the time frame of this study which embraced five years.

Knowledge of the spatial pattern, fecundity, and population dynamics of each of the coral-reef starfish species represented is essential to an understanding of the stability or otherwise of the populations of species comprising the coral-reef asteroid assemblages of Indo-West Pacific reefs. This knowledge is also essential to an understanding of outbreak phenomena, such as population outbreaks of Acanthaster planci. The obtaining of comparative distribution and reproductive data on many starfish species from Heron Reef will clarify the factors that influence diversity and stability within this assemblage.

CHAPTER 2. SPECIES PRESENT

2.1 Introduction

An initial study of the echinoderms of the Great Barrier Reef was conducted by H.L.Clark during a visit to the Murray Islands in 1913 (Clark, 1921). This work was followed by that of A.A.Livingstone during the Great Barrier Reef Expedition (Livingstone, 1932) and that of Gibbs, Clark and Clark (1976). Two monographs dealing with the Australian echinoderm fauna were compiled by H.L.Clark (Clark, 1938; 1946). Extensive biogeographical studies of Queensland echinoderms were undertaken by Endean (1953; 1956; 1957; 1961; 1965) and many of the records therein relate to Heron Island asteroids.

In the Indian Ocean, a detailed account of the echinoderm species present in West Australian waters was provided by Marsh (1976). Elsewhere in the Indian Ocean, the asteroid (starfish) fauna has been studied at Mozambique (Jangoux, 1972 a; Walenkamp, 1990), South Africa (Thandar, 1989), Somalia (Tortonese, 1980), the Gulf of Suez (James and Pearce, 1969), the Red Sea (Clark, 1967 a; Tortonese, 1960, 1977, 1979), the Arabian Gulf (Price, 1981), the Iranian Gulf (Mortensen, 1940), India (Koehler, 1910; James, 1973), the Andaman and Nicobar Islands (Julka and Das, 1978) and the Maldive Islands (Clark and Spencer-Davis, 1966; Jangoux and Aziz, 1985).

In the Pacific Ocean, the starfish fauna has been studied in China (Liao, 1980), Hong Kong (Clark, 1982), Taiwan (Chao and Chang, 1989), the Philippines (Fisher, 1919; Domantay, 1972; De Celis, 1980), the Ryukyu Islands (Hayashi, 1938 a), the Ogasawara Islands (Hayashi, 1938 b), the Caroline Islands (Hayashi, 1938 c; Grosenbaugh, 1981; Marsh, 1977; Oguro, 1984), the Mariana Islands (Yamaguchi, 1975 b; Kerr et al., 1992), the Marshall Islands (Clark, 1952), Indonesia (Guille and Jangoux, 1978; Jangoux, 1978), New Caledonia (Jangoux, 1984), Tonga (Clark, 1931), South East Polynesia (Marsh, 1974), Hawaii (Fisher, 1906; Ely, 1942) and the general North Pacific region (Fisher, 1911, 1925). The geographical distribution of the shallow water species was reviewed by Clark and Rowe (1971).

There have been many taxonomic revisions within the Asteroidea. The works of Baker and Marsh (1974), Blake (1979; 1980; 1981; 1983; 1990), Jangoux (1972 b; 1980), Pope and Rowe (1977), Rowe (1977) and Marsh (1991) have included species of coral-reef starfish. All previous revisions were summarised in the specific descriptions and keys to the asteroid species provided by Clark and Rowe (1971).

2.2 Methods

Specimens of several species of starfish were required primarily for size-frequency and reproductive analysis. Sampling methods were chosen so as to ensure that the sample sizes were sufficient to allow statistical analysis of size-frequency and reproductive data in a reasonable number of species. Starfish were collected by means of quadrats, general searches and on traverses that were conducted primarily at the western end of Heron Reef (Figure 1). On Heron Reef, traverses ran between the cay and the reef crest (0.5 to 2 kilometres apart) and also between two points both on the reef crest (0.5 to 6 kilometres apart). Because the primary purpose of sampling was the collection of size-frequency and reproductive data, the traverses were not stratified with respect to habitat. Traverses were neither systematic nor random and most traverses included both reef flat and reef crest zones. All exposed starfish within a four-meter width were collected for the length of the traverse. In addition to the collection of exposed starfish, a selection of large and small, dead coral slabs was overturned and cryptic specimens located beneath these slabs were collected. The lagoon and its adjacent coral pools were not sampled by traverse because of the difficulty in traversing this habitat.

All traverses were conducted within two hours of low tide, during the period of spring tides (full or new moon). When the water over the reef flat and reef crest was any deeper than this or under adverse weather conditions it was difficult to locate smaller starfish. Specimens that were required for reproductive studies were collected during general searches at these times but these specimens were not included in either the abundance or size-frequency data because this would have been biased towards the more visible species and individuals.

In total, 72 overlapping, intertidal traverses were conducted during the period from May 1978 to December 1982. The total area sampled by these traverses was approximately 120 hectares (1.2 square kilometres) which is equivalent to about five percent of the shallow-water, reef area of Heron Reef. The mean traverse length was just over four kilometres.

Cryptic species were also sampled using metre square quadrats in particular areas where previous traverse sampling had shown that starfish abundance was relatively high. These samples provided data for starfish present on a very small area of the reef crest. These quadrat samples cannot be regarded as random, and they are not typical of the reef crest in general. The reef crest zone is extremely variable and spatial heterogeneity (patchiness) appeared to be highly

dependent on the scale of sampling. These quadrat samples were undertaken to obtain estimates of the starfish density in these localised patches.

Subtidal specimens of starfish were collected on the reef slope and off-reef floor by the use of SCUBA. These subtidal samples were not used to determine subtidal starfish density because limitations in underwater visibility would have resulted in the underestimation of all starfish abundances. Detailed quadrat sampling would not have been directly comparable with intertidal traverse data and such sampling was not considered appropriate given the logistical constraints of extensive sampling using SCUBA. The off-reef floor was only rarely sampled and the species that occur in this habitat may be much more abundant than is apparent from the results obtained.

All starfish were identified, measured and placed along with conspecifics in glass aquaria at the Heron Island Research Station. Specimens were identified by reference to Clark and Rowe (1971). Specimens were also compared with their original descriptions where necessary. An examination of the specimens with a stereoscopic microscope was sufficient to distinguish all species. Juvenile identification was possible in all cases by reference to Clark (1921), Yamaguchi and Lucas (1984) or Yamaguchi (1973 a, 1973 b, 1974, 1977 a).

All individuals not required for taxonomic study were released in habitats similar to those where they were found. Specimens of all species studied were photographed live and some were preserved in alcohol. These are housed in the Department of Zoology, University of Queensland.

Throughout this thesis, unless some ecological parameter is given higher priority temporarily, the sequence in which species appear in tables is determined by their systematic position. The families are sequenced according to Blake (1979, 1980, 1981, 1987, 1990) and the classification of Clark and Rowe (1971). The genera are sequenced alphabetically within families.

2.3 Results

The species listed in Table 2.1 have either been recorded previously from Heron Reef or were found in the present study and represent new records for the locality (marked with "*"). The species included are all those that occur either on the reef top (reef flat and reef crest) or on the reef slope extending to a depth of approximately 30 metres. At

Heron Reef this is approximately the depth where the substrate of predominantly live coral or coral rubble changes to the finer sediments of the off-reef floor. Coral-reef species that do not appear to occur on the off-reef floor are marked “+”.

Table 2.1 Asteroid species recorded from Heron Reef.

Astropectinidae
Astropecten polyacanthus Muller and Troschel,1842

Goniasteridae
Iconaster longimanus (Mobius, 1859) *

Oreasteridae
Culcita novaeguineae Muller and Troschel,1842 +

Acanthasteridae
Acanthaster planci (Linnaeus,1758) +

Asteropseidae
Asteropsis carinifera (Lamarck,1816) *+

Ophidiasteridae
Dactylosaster cylindricus (Lamarck,1816) *+
Fromia elegans Clark,1921 *+
Fromia milleporella (Lamarck,1816) +
Gomophia egyptiaca Gray,1840 +
Linckia guildingii Gray,1840 +
Linckia laevigata (Linnaeus,1758) +
Linckia multifora (Lamarck,1816) *+
Nardoa novaecaledoniae (Perrier,1875) +
Nardoa pauciforis (von Martens,1866) +
Nardoa rosea Clark,1921
Neoferdina cumingi (Gray,1840) +
Ophidiaster armatus Koehler,1910 *
Ophidiaster confertus Clark,1916
Ophidiaster granifer Lutken,1871 +
Ophidiaster lioderma Clark,1921 *+
Ophidiaster robillardi de Loriel,1885 *+
Ophidiaster watsoni (Livingstone,1936) +
Tamaria megaloplax (Bell,1884) *

Asterinidae
Anseropoda rosacea (Lamarck,1816)
Asterina anomala Clark,1921 *+
Asterina burtoni Gray,1840 +
Disasterina abnormalis Perrier,1876 *+
Disasterina leptalacantha (Clark,1916) +
Tegulaster emburyi Livingstone,1933 *+

Mithrodiidae
Mithrodia clavigera (Lamarck,1816) *+

Echinasteridae
Echinaster luzonicus (Gray,1840) +
Echinaster stereosomus Fisher,1913 *

Asteriidae
Coscinasterias calamaria (Gray,1840) *

* New record for Heron Reef + coral-reef species

In addition to the preceding species, Anthenea aspera, Stellaster equestris, Metrodira subulata and Acanthaster brevispinus were recorded from the area by Bennett (1958). These species were dredged from a depth of 45 meters east of Wistari Reef and were not directly associated with any coral-reef habitat. Halityle regularis was recorded by Baker and Marsh (1974) and Andora popei was recorded by Rowe (1977) from the off-reef floor near Heron Reef. Pentaceraster regulus and Euretaster insignis were also observed on the off-reef floor.

The following brief notes relate to the species of starfish that have been located at Heron Reef (on the reef flat, reef crest or reef slope) either in this study or by previous workers.

Family Astropectinidae
Astropecten polyacanthus Muller and Troschel,1842

This species of starfish is not restricted to coral reefs but occurs also in sandy areas along the east coast of the Australian mainland. It was not common, but specimens were found during this study in the deeper waters of the off-reef floor. It is recognised by the many conspicuous sharp spines along the body margin. The tube feet do not possess suckers at their tips. It has been found on a sandy spit at Heron Island Reef by Endean (1965).

Family Goniasteridae
Iconaster longimanus (Mobius,1859)

This orange and white patterned starfish is immediately recognised by its long tapering arms. It was not common at either Heron or the adjacent Wistari Reef, but specimens were located during this study in about 20 metres of water on the deeper parts of the reef slope. They were usually associated with coral rubble. Some specimens that were collected had recently lost one arm.

Family Oreasteridae
Culcita novaeguineae Muller and Troschel,1842

The juveniles of this species (R less than 70 mm) look quite different from adults. This starfish is most commonly encountered on the reef flat although it occurs also on the reef crest. Its greatest abundance may be at the base of the reef slope or in the deeper coral pools adjacent to the lagoon. This large and conspicuous species was not common on the traverses at Heron Reef during the period of this study.

Family Acanthasteridae
Acanthaster planci (Linnaeus,1758)

This well-known species was uncommon at Heron and the adjacent Wistari Reef during the period of the present study. Only five subtidal adults and one juvenile specimen were encountered. Endean (1961) recorded a single specimen from a pool near the reef crest at Heron Reef.

Family Asteropseidae
Asteropsis carinifera (Lamarck,1816)

This species is not common at the southern end of the Great Barrier Reef. It has been recorded as common at Mer in the Murray Islands (Clark, 1921). During this study, three specimens were encountered on the reef crest at Heron Reef.

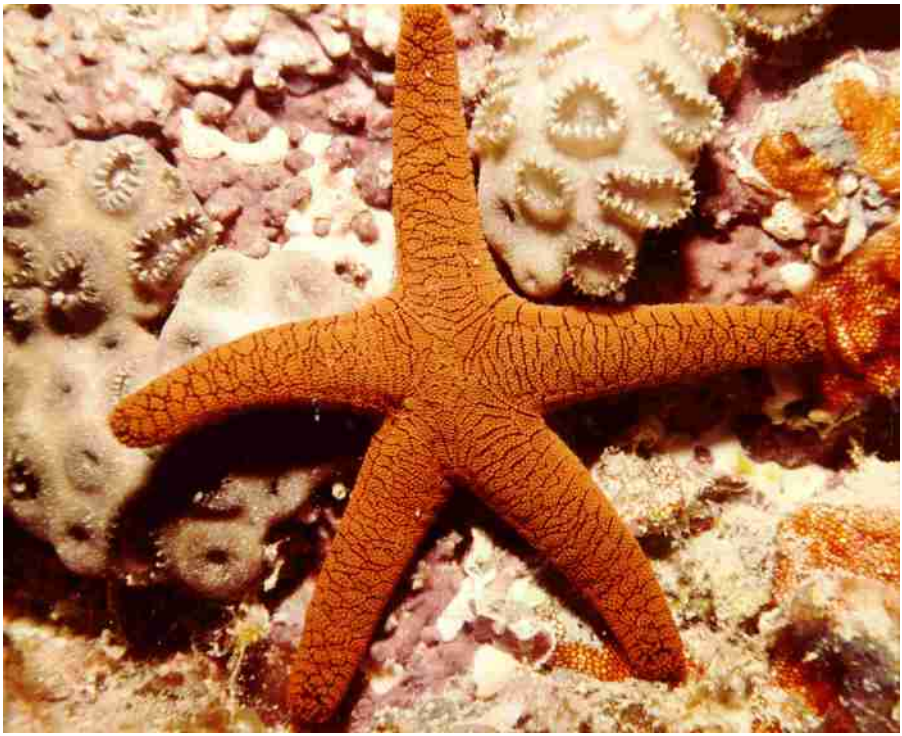
Family Ophidiasteridae
Dactylosaster cylindricus (Lamarck,1816)

During this study, a single specimen was located on the reef crest at Heron Reef. Few specimens of this species have been found on the Great Barrier Reef or elsewhere throughout its range. This species can be distinguished from others in this family by the presence of only a few small granules in the centre of each plate of the body. The remaining granules are concealed by a skin-like membrane. It occurs on the rocky reefs off southern Queensland more frequently than it does at Heron Reef.

Fromia milleporella (Lamarck,1816)

One specimen was found on the reef crest. Endean (1956) found two specimens under boulders on the reef crest.

Fromia elegans Clark,1921

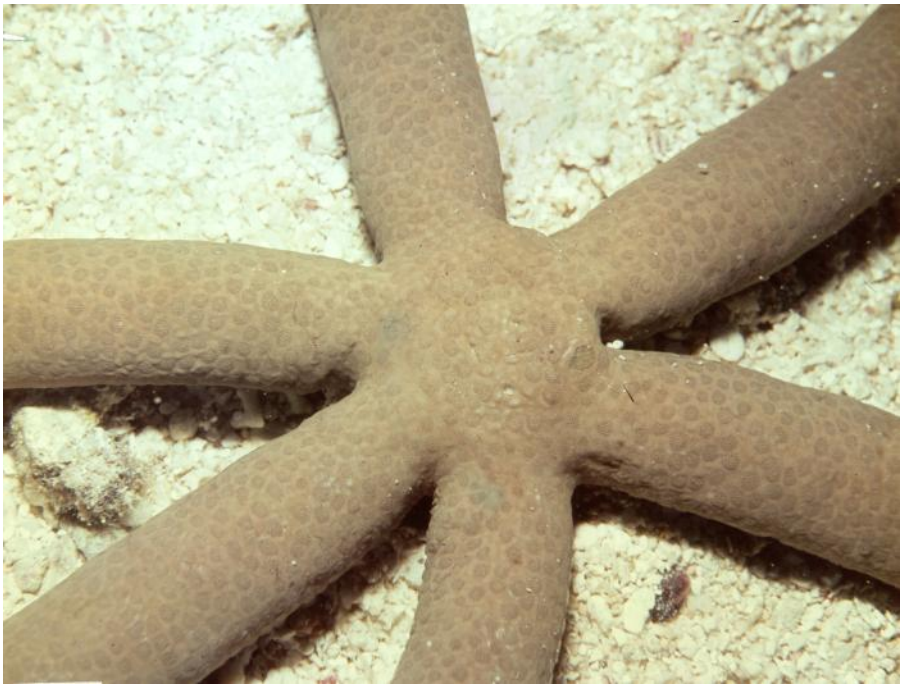


At Heron Reef, this starfish is relatively common in the reef slope zone. Most specimens have five even arms, but specimens with four and six arms were not uncommon. This species was found also on the reef crest lying exposed in small pools, and on the sand at the base of the reef slope in 20 metres of water.

Gomophia egyptiaca Gray,1840

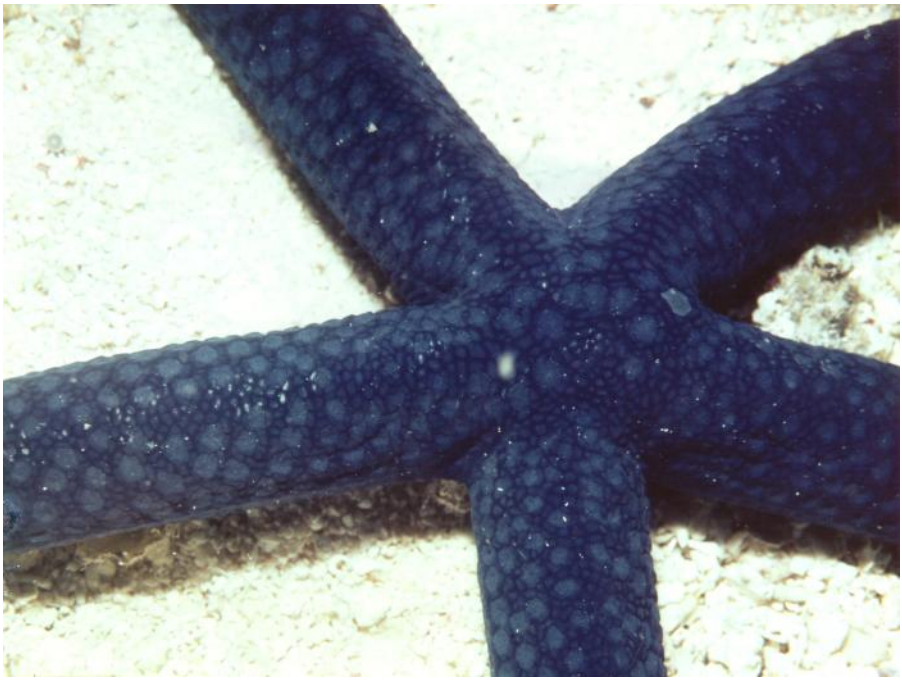
At Heron Reef, the only individuals encountered, during this study, were coloured purple and brown with pink tips to the tubercles which cover the aboral surface of the body. Specimens of this species were usually found either concealed under boulders on the reef crest or crawling amongst dead coral rubble on the reef slope. This species is not common at Heron Reef. Of the small number of intertidal specimens collected, two were found in close proximity. Endean (1965) found only two specimens on the reef flat at Heron Reef.

Linckia guildingii Gray,1840



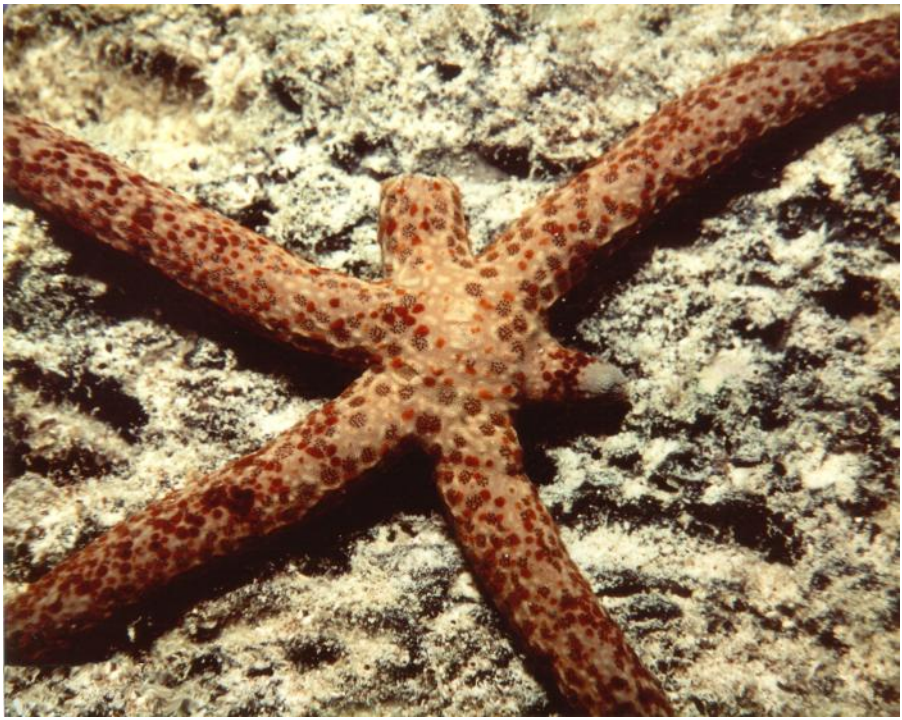
The Grey Linckia, while not as common as L. laevigata or L. multifora, is encountered frequently on reefs of the Great Barrier Reef. The grey coloration conceals the animal when crawling over dead coral clumps which are covered by filamentous algae, but the animal is conspicuous when on coral sand. Although the adult starfish is uniform grey in colour, juveniles are mottled white, grey and purple, and do not lose this appearance until a size of about 80 mm arm radius is attained.

Linckia laevigata (Linnaeus,1758)



The Blue Linckia inhabits intertidal reef areas throughout the Indo-West Pacific region. It attains a large size (arm radius 180 mm), is brightly coloured, and is usually found lying unconcealed on or near coral clumps in the reef flat. It can be found also on the reef crest, lying either exposed on the algal rim or partially hidden under coral boulders in the rubble zone. There is very little colour variation within this species on the Great Barrier Reef. The most frequent number of arms is five although arm number ranges from three to seven. The extremes are rare.

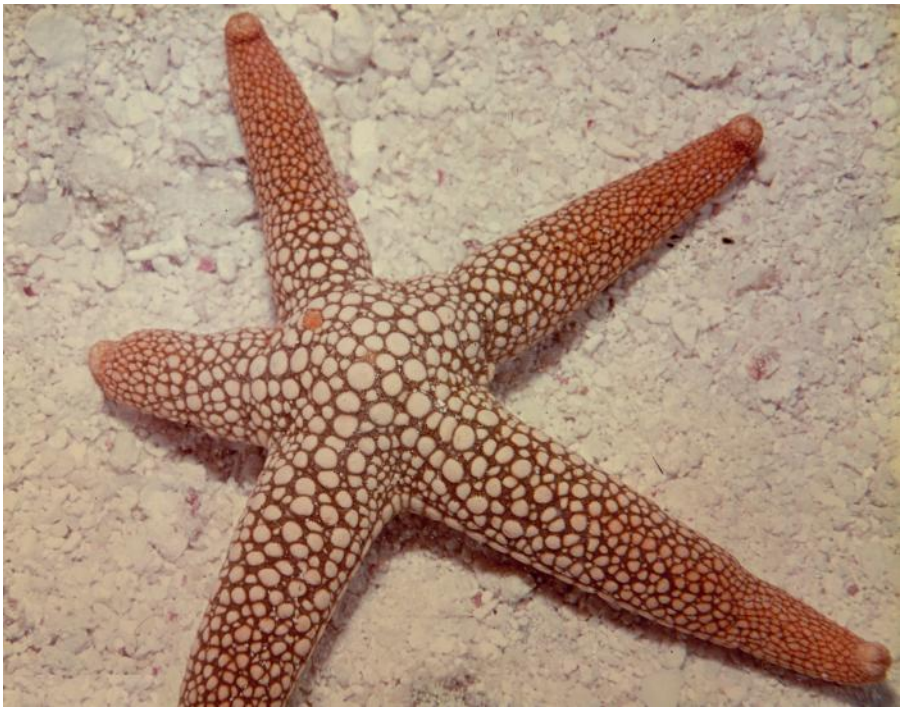
Linckia multifora (Lamarck,1816)



This species is usually found with one or more arms missing, these having been autotomised. The maximum size that this animal attains at Heron Reef is about 100 mm arm radius, but most specimens are approximately one-third this size. Sometimes the starfish will be found crawling in the open across the reef crest but more often it will be found under boulders. The specimens which occur under boulders are usually smaller and lighter in colour and do not have the brown coloration which is found in those that have adopted an exposed existence. The most common number of arms is six but the number varies between three and eight. It is unusual to find a specimen with all arms of equal length.

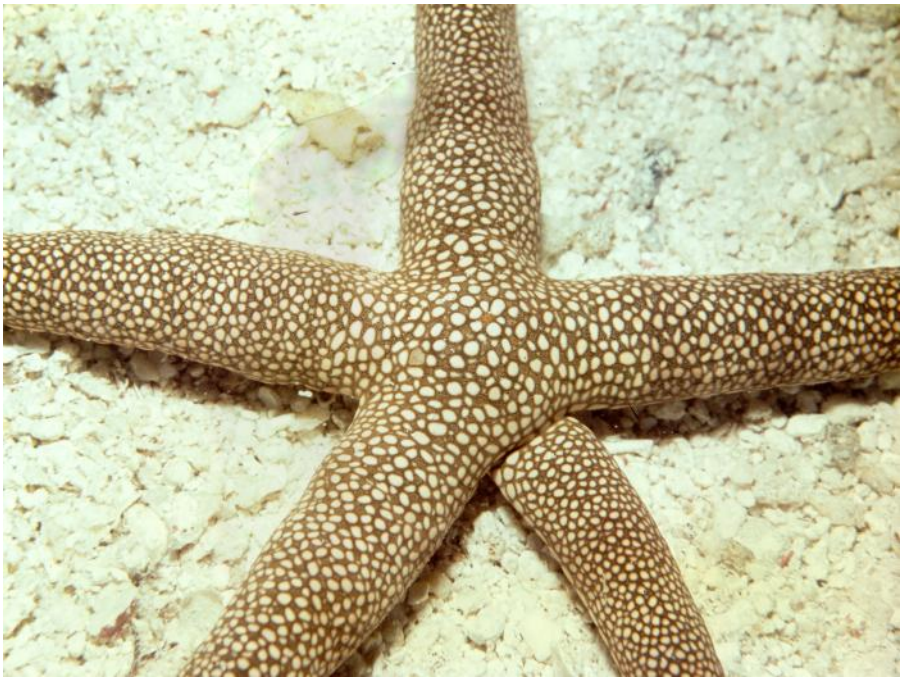
Occasionally specimens are found that do not belong clearly to either Linckia laevigata or Linckia multifora. These specimens are blue in colour but have pointed arms and show evidence of recent autotomous reproduction. There is a small row of granules between the furrow spines. One blue comet form has been found during this study. Because of their general morphology, these specimens have not been regarded as Linckia laevigata, but as colour variations of Linckia multifora.

Nardoa novaecaledoniae (Perrier,1875)



The two common species of Nardoa appear quite similar in overall appearance and differ in the arrangement of the plates which cover the arms. In Nardoa novaecaledoniae these plates are abruptly reduced in size in the outer one-third of each arm.

Nardoa pauciforis (von Martens,1866)



This starfish is slightly less common than the previous species but is not hard to find on Heron Reef. It occurs more commonly on the reef flat than on the reef crest but it can be overlooked in this habitat as both N. pauciforis and N. novaecaledoniae blend well with the background of living and dead coral. The animals are most conspicuous when crawling over the sand between coral clumps. The average individual size of this species is slightly larger than that of N. novaecaledoniae. Also, the arms are usually longer relative to the body than in N. novaecaledoniae. A diagnostic feature of N. pauciforis is the absence of an abrupt change in the size of the plates towards the outer one-third of the arms.

Nardoa rosea Clark,1921

This species is more frequently encountered in the deeper parts of the reef slope (20 meters) than on the top of the reef at Heron Reef but is not common in any of these habitats. It is a beautiful starfish with an average size of 90 mm radius.

Neoferdina cumingi (Gray,1840)

This starfish is not encountered often on the reef top at Heron Reef but is occasionally seen when diving on the reef slope. There is great variation in the number and pattern of the red spots which are conspicuous along the arms.

Ophidiaster armatus Koehler,1910

All members of the genus Ophidiaster possess four rows of papular areas on both sides of every arm, a total of eight rows per arm. Papulae are the respiratory organs and occur in groups of between five and twenty, each appearing as a small, transparent projection through the outside body wall. The extent to which each papula is extended is dependent greatly on the water conditions.

O. armatus is readily recognisable by its dark coloration, tapering arms and by the coarse feel of the animal due to the very rough granulation of its skin. This species is found in low numbers, mainly at the base of the reef slope at Heron Reef.

Ophidiaster granifer Lutken,1871
This species possesses the tapering arms and uneven granulation of

the previous species, but it is easily distinguished by its general coloration, smaller size (25 mm) and shorter arms relative to the diameter of the disc. Specimens of this species are usually encountered under boulders on the reef crest where they occur with moderate abundance. They are always cryptic in their habits.

Ophidiaster lioderma Clark,1921

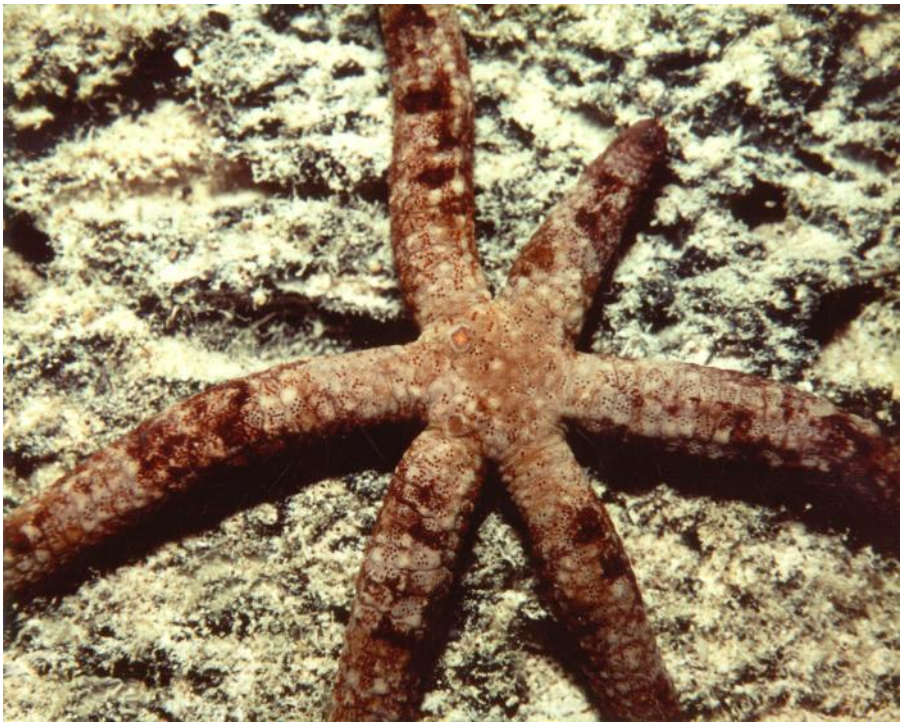
This moderate sized starfish (R=100 mm) is very rare indeed having been found on two known occasions only, in two localities which are far apart on the Great Barrier Reef. The original specimen was discovered by H.L.Clark when he visited the northern end of the reef and was based at Murray Island in Torres Strait at the turn of the century. During this study, a further specimen was located on the reef crest at Heron Reef and is now housed in the West Australian Museum.

This species is a medium brown in colour and can be readily identified by the skin covered body which possesses microscopic granulation. The only other member of this family which has a covering of thick skin is Leiaster leachi, but this species has no surface granulation whatsoever and is brightly coloured.

Ophidiaster confertus Clark,1916

Four specimens of this species were located on the reef crest at Heron Reef. This species which grows up to 160 mm arm radius occurs more commonly on the New South Wales coast than at the southern end of the Great Barrier Reef (Clark, 1946).

Ophidiaster robillardi de Loriel,1885



This species occurs in moderate abundance in patches at Heron Island. The extreme patchiness of the distribution and abundance of this species is attributable to low dispersion associated with asexual reproduction. The average size of specimens is 35 mm arm radius and about ten percent of the specimens encountered were comet forms resulting from autotomous reproduction.

Ophidiaster watsoni Livingstone,1936

Gomophia egyptiaca and Ophidiaster watsoni are very similar and may be conspecific. Endean (1956) found one specimen of O. watsoni under a boulder on the reef edge at Heron Island.

Tamaria megaloplax (Bell,1884)

This species is found in the deeper waters, on sand near the base of the reef slope at Heron Reef. It occurs much more commonly on rocky reefs in south-east Queensland, than it does on the Great Barrier Reef. The average size of specimens found in south-east Queensland is about 100 mm arm radius. The specimens show considerable variation in the degree of roundness of the plates on the arms. This genus is characterised by having only three parallel rows of papular groups on both side of each arm, unlike Ophidiaster which has four, and Hacelia which has five rows.

Family Asterinidae
Anseropoda rosacea (Lamarck, 1816)

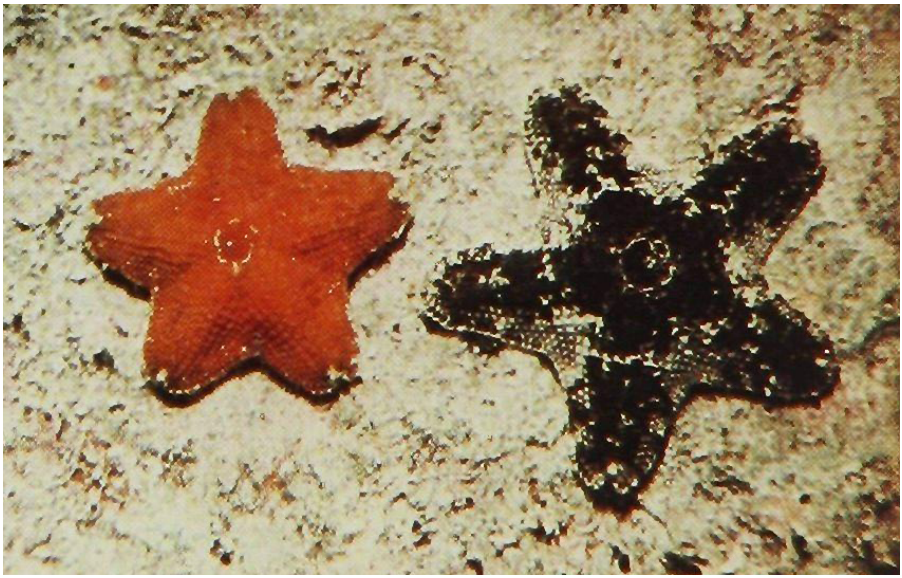
A single specimen of this species was found on sand in a reef-crest pool at Heron Reef by Endean (1956).

Asterina anomala Clark,1921

This small starfish is usually hard to find as the maximum size of individuals found on the Great Barrier Reef is about 5 mm arm radius. The bright coloration is of little help in finding this species as the boulders under which it occurs are encrusted usually with other brightly coloured invertebrates such as sponges and ascidians. This species is probably much more common than it appears to be but its small size makes sampling extremely difficult.

The usual number of arms in this species is seven. Half of these are normally regenerating as this species reproduces by binary fission. In this process, the animal divides into two and both sides regenerate the missing arms. If the regeneration has not proceeded very far then three or four adjacent ambulacral grooves will not extend much beyond the mouth.

Asterina burtoni Gray,1840



The taxonomic positions of this and of the preceding species are not clear. While the coloration of Asterina burtoni is quite variable, ranging from grey, through green to red or purple, it does not exhibit the multi-coloured pattern possessed by the previous species. A. burtoni does not reproduce by fission at Heron Reef and consequently most specimens have five arms of equal length. The average size of specimens is 13 mm arm radius.

Disasterina abnormalis Perrier,1876

This species has been recorded at a few localities along the Great Barrier Reef, and also in Indonesia as well as in the South Pacific. When alive, the animal is covered by a relatively thick skin which conceals the underlying plates. Many of these plates bear some very short rounded spines but it is not possible to discern the diagnostic characters of this species unless the specimen is preserved and then dried.

At Heron Reef at the southern end of The Great Barrier Reef, this is the most abundant starfish found on the top of the reef. It lives amongst the broken coral rubble on the innermost portion of the reef crest. The average size of specimens is 15 mm arm radius, but this size varies with periods of growth and with recruitment of juveniles to the population.

Disasterina leptalacantha (Clark,1916)

This close relative of the preceding species grows to the same size, but is known only from the Capricorn Group at the southern end of the Great Barrier Reef. The difference between these two species is unmistakable as Disasterina leptalacantha possesses very long, extremely thin spines along the body margin, but in life these may be folded upwards against the side of the body and are overlooked easily. The coloration of this species is different from that of the previous one and the arms are also slightly longer. The reason for the apparent limited distribution of this species is unknown.

The main habitat of this species is amongst the broken slabs of beachrock at low tide level. It is not common but specimens will be found either adhering to the underside of the rocks or amongst the sand immediately under the rocks.

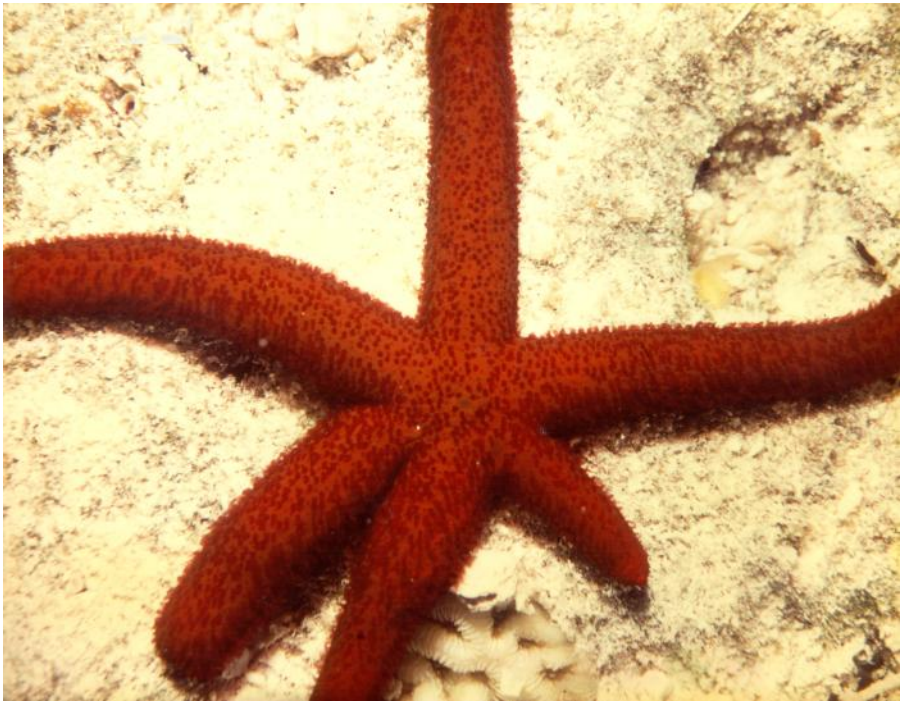
Tegulaster emburyi Livingstone,1933

During this study, one specimen of this species was located on the reef crest at Heron Reef. The only other known specimen of this species was found at North-West Island, also in the Capricorn Group. Both specimens were found under a dead coral boulder in the reef crest zone. This species is exceedingly rare and may also be highly restricted in its geographic range. Both known specimens were just under 20 mm in arm radius.

Family Mithrodiidae
Mithrodia clavigera (Lamarck,1816)

During this study, one specimen was located at Heron Reef, but it did not occur within the intertidal traverses. It was located on the reef crest in December 1984. The species has been found elsewhere in the South Pacific but is uncommon.

Family Echinasteridae
Echinaster luzonicus (Gray,1840)



This starfish ranges from almost black, through red, to speckled orange and black in coloration. Specimens with all arms of equal length are not common as this species reproduces by means of autotomy, and comet forms will be found along with the adults in most habitats. The habitat in which this species is most abundant is under coral boulders on the reef crest. However, specimens may be found in most other intertidal habitats as well as on the reef slope and extending down to the boundary with the off-reef floor. The specimens which are found sub-tidally are larger usually than those found intertidally. The average size of specimens varies from one reef zone to another, but on the reef crest it is about 47 mm arm radius. However, its size is dependent on the amount of autotomy which has occurred recently. The species can grow to about 90 mm. Some of the specimens encountered at the edge of the off-reef floor possess epiphytic ctenophores crawling over the arms of the starfish.

Echinaster stereosomus Fisher,1913

At Heron Reef, this species is found near the base of the reef slope. It occurs on the rocky reefs off southern Queensland more frequently than it does at Heron Reef.

Family Asteriidae
Coscinasterias calamaria (Gray,1840)

This is primarily a southern species (Clark, 1946). Barrier Reef specimens are small, up to 30 mm arm radius, compared with the much larger individuals found on the mainland coast. This species is capable of asexual reproduction by binary fission. At Heron Reef, C. calamaria maintains small patches of moderate abundance by asexual reproduction. Indeed, it appears unlikely that specimens grow sufficiently large to become sexually mature at Heron Reef.

2.4 Discussion

The following species represent new records for Heron Reef:

Iconaster longimanus, Asteropsis carinifera, Dactylosaster cylindricus, Fromia elegans, Linckia multifora, Ophidiaster armatus, Ophidiaster lioderma, Ophidiaster robillardi, Tamaria megaloplax, Asterina anomala, Disasterina abnormalis, Tegulaster emburyi, Mithrodia clavigera, Echinaster stereosomus and Coscinasterias calamaria.

This study has provided the most southerly records from Great Barrier Reef waters of Iconaster longimanus, Asteropsis carinifera, Dactylosaster cylindricus, Fromia elegans, Linckia multifora, Ophidiaster armatus, Ophidiaster lioderma, Ophidiaster robillardi, Tamaria megaloplax, Asterina anomala, Disasterina abnormalis, Mithrodia clavigera and Echinaster stereosomus.

Single specimens of both Ophidiaster lioderma and Tegulaster emburyi were recorded at Heron Reef during this study and these represent the only known specimens of these species apart from their holotypes. Additionally, this study has provided the first record of the predominantly temperate species, Coscinasterias calamaria on the Great Barrier Reef. Euretaster insignis, which has not been recorded in the vicinity of a reef of the Great Barrier Reef, was found on the off-reef floor between Heron and Wistari Reefs.

Ophidiaster watsoni and Anseropoda rosacea were recorded from Heron Reef by Endean (1957) but were not located during this study. The taxonomic position of the former species is unclear. Anseropoda rosacea either is very uncommon at present, or primarily inhabits the sandy bottom of the lagoon which was not sampled extensively. Ophidiaster hemprichi and Ophidiaster lorioli occur at Heron Reef (Marsh pers. com.) but were not located during this study. Halityle regularis and Andora popei have been recorded from the off-reef floor in the vicinity of Heron Reef, by Baker and Marsh (1974) and Rowe (1977) respectively. These species were not located during this study as the off-reef floor was not sampled as intensively as were the shallow-water zones.

Because of its southerly position on the Great Barrier Reef, some predominantly sub-tropical asteroid species (e.g. Ophidiaster confertus and Coscinasterias calamaria) occur at Heron Reef but appear to not occur further north on the Great Barrier Reef. Additionally, some predominantly mainland species (Endean, 1957) occur either on, or in close proximity to, reefs of the Great Barrier

Reef. The biogeographical study of Endean (1957) has shown that a distinction must be made between the asteroid species which occur predominantly on coral reefs of the Great Barrier Reef and those which occur elsewhere in Queensland waters. The results of the present study are in accord with this view. Clearly, there is a coral-reef asteroid fauna exemplified by that of Heron Reef, which is different from that of off-reef waters. However, as noted by Endean (1957), some species which occur on reefs of the Great Barrier Reef are not exclusively coral-reef species. For example, species such as Archaster typicus, Protoreaster nodosus, Ophidiaster confertus, Tamaria megaloplax, Asterina nuda, Patiriella pseudoexigua, Anseropoda rosacea and Coscinasterias calamaria occur predominantly in habitats other than those provided by coral reefs.

It seems likely, because of the extremely southern position of Heron Reef and other reefs in the Capricorn and Bunker Group, that many of the predominantly coral-reef species do not occur there with the same abundance as they do further north where physical conditions such as low water temperature on the reef flat in winter may be less extreme. Additionally, the relative isolation of this group of islands and reefs from the rest of the Great Barrier Reef might influence the abundance of those species with a low capacity for larval dispersal. However, these factors do not appear to affect the abundance of species that are common throughout the Great Barrier Reef. At higher latitudes, such as that of Heron Reef, the factors just mentioned might increase the abundance range between the most common and the rarest species. This would be reflected in the extent of sampling that would be required to locate most of the species that occur in the locality.

When current asteroid species lists for Heron Island and other reefs of the Capricorn Group are compared with those of recent studies of the North Pacific coral-reef Asteroidea (Yamaguchi, 1975 b; Marsh, 1977) it is apparent that some of the species that occur at Guam or Palau (e.g. Archaster typicus, Celerina heffernani, Fromia indica, Fromia monilis, Nardoa tuberculata, Nardoa tumulosa, Neoferdina offreti, Asterina corallicola and Echinaster callosus), have not been recorded from the Capricorn Group. On the other hand, some of the species that have been recorded from Heron Island and other reefs of the Capricorn Group (e.g. Tosia queenslandensis, Iconaster longimanus, Fromia elegans, Nardoa pauciforis, Nardoa rosea, Neoferdina cumingi, Ophidiaster armatus, Ophidiaster lioderma, Disasterina abnormalis, Disasterina leptalacantha and Tegulaster emburyi), have not been recorded from either Guam or Palau.

Future investigations may reveal that some of the above similar but geographically separated coral-reef species (e.g. Fromia indica and Fromia elegans) are conspecific. However, future investigations may also confirm the restricted distributions of some of the species mentioned above.

Most of the coral-reef asteroids found on the Great Barrier Reef, including Heron Reef and other reefs of the Capricorn Group, have strong affinities with coral-reef asteroids of the Western Pacific region as noted by Endean (1957). However, a few species appear endemic to the reefs of the Capricorn Group or are essentially sub-tropical species that have extended their ranges to include the southernmost reefs of the Great Barrier Reef.

CHAPTER 3. HABITAT

3.1 Introduction

The spatial distribution of coral-reef starfish has been studied at several different scales. The physical, biological and historical parameters that explain the distribution of these species on the global scale (Clark and Rowe, 1971) will not directly explain the spatial pattern of an assemblage on a single reef. The small-scale distribution of Linckia laevigata on the fringing reef at Guam, and some factors which determine the abundance of this species in different habitats, were described by Strong (1975). The distribution and movements of Linckia laevigata at Lizard Island were examined by Thompson and Thompson (1982). Laxton (1974) suggested that Linckia laevigata may alter its distribution following outbreaks of Acanthaster planci. The distribution of an assemblage of starfish on a reef that is not known to have undergone outbreaks of Acanthaster planci has not been studied previously.

Feeding of starfish was extensively reviewed by Sloan (1980) and Jangoux (1982) and there have been many detailed examinations of the diets, competitive interactions and niche separation of colder water species (Blankley, 1984; Menge, 1972 a, 1972 b, 1981; Menge and Menge, 1974). The ecology of the tropical omnivorous, Atlantic species Oreaster reticulatus has been extensively studied by Scheibling (1980, 1981 a, b, 1982). The known diets and habitat preferences of the Indo-West Pacific coral-reef species have been tabled by Yamaguchi (1975 b). The contribution of these aspects of niche specialisation to the co-existence of many asteroid species in the coral reef ecosystem is poorly understood.

The general correlation between food supply and growth in asteroids has been discussed (Mead, 1900; Wolda, 1970; Paine, 1976). Species such as Acanthaster planci and Culcita novaeguineae are known to prey on hard corals (Endean, 1969; Yamaguchi, 1975 b; Glynn and Krupp, 1986). The response of Acanthaster planci to different prey species has been studied (Ormond, Hanscomb and Beach, 1976). Asterina anomala, Asterina burtoni, Ophidiaster granifer and Gomophia egyptiaca are known to feed on sponges and ascidians (Thomassin, 1976; Yamaguchi, 1975 b) while Astropecten polyacanthus and other members of its genus are known to prey on molluscs (Christensen, 1970; Ribi and Jost, 1978; Jost, 1979). Coscinasterias calamaria along with most members of the Order Forcipulatida, which are primarily inhabitants of temperate waters, are known to also prey on molluscs (Sloan, 1980; Jangoux, 1982).

However, the vast majority of coral-reef starfish are thought to be general detritovores and to feed primarily on the epibenthic felt (Thomassin, 1976) which is widely distributed throughout the reef environment. The possibility of ciliary nutrition (filter feeding) in some asteroids was raised by Gemmill (1915).

With the exception of what were once considered "primitive" genera such as Astropecten and Luidia (see Blake, 1987), starfish generally feed by everting their stomach over the substrate and digestion is external (Blake, 1990). However, the forcipulate species Heliaster helianthus is known to possess a flexible feeding habit involving both intra-oral and extra-oral feeding (Tokeshi, 1991). When Acanthaster planci and Culcita novaeguineae feed on hard coral they evert their stomachs and leave white feeding scars where the living tissue has been digested off the skeleton (Yamaguchi, 1975 b). Predominantly epibenthic feeders such as members of the genera Linckia, Nardoa and Ophidiaster leave no such feeding mark to indicate the position of their everted stomach when they are removed from the substrate while feeding (Yamaguchi, 1975 b).

While there have been extensive studies of the micro-habitat requirements of some coral-reef animals, for example gastropods (see e.g. Kohn and Leviten, 1976; Leviten and Kohn, 1980; Reichelt, 1982) there has been little work done on this aspect of coral-reef asteroid ecology. The role of habitat complexity in determining the population densities of species of gastropod within the coral reef ecosystem was discussed by Kohn (1968). However, the temporal scale of many community studies is often insufficient to determine the stability, or otherwise, of the observed community structure.

The degree to which species specialise in their use of habitat and other resources is a major component of the complexity of any assemblage (Klopfer, 1959; Klopfer and MacArthur, 1960, 1961; MacArthur and Levins, 1964, 1967; May and MacArthur, 1972. Reichelt (1982) regarded the availability of refuges from predation, desiccation and turbulence as determining factors in the spatial pattern of many intertidal species of gastropod. Kohn (1968) suggested that habitat complexity and the resultant spatial heterogeneity may directly determine the diversity of species assemblages.

Other authors have stated that the species assemblages that they examined were predominantly random. Guilds of species which use their habitat in a similar fashion were proposed by Sale (1976, 1977). In determining the spatial distribution of organisms, many authors propose the use of null (or neutral) models to prevent random events

from being misinterpreted as meaningful biological pattern (Connor and Simberloff, 1979; McGuinness, 1984). However, caution over the misuse of inappropriate null models, which incorrectly reject real pattern, has been suggested by other authors (Dunbar, 1980; Quinn and Dunham, 1983; Roughgarden, 1983; Gilpin and Diamond, 1982).

3.2 Methods

At the completion of each traverse, all specimens were identified, counted and measured. The estimated area of the traverse was also recorded. While traverses were not stratified with respect to habitat, the zone of maximum density (primary habitat) was quite apparent for some species. Where a species occurred in more than one zone, the zones of less-frequent occurrence were referred to as secondary habitats. The distinction between primary and secondary habitat was much clearer in some species than in others. Some species were found so rarely that their range of habitat is unknown. In these cases, the zone in which they were located is regarded as the primary habitat.

25 specimens of Linckia laevigata were tagged with small plastic clothing tags which were inserted through the body wall of one arm, near its base, in such a way that a number inscribed on each tag was visible on close examination of the specimen. These starfish were then released at a site that provided no refuge other than under boulders. All boulders within a radius of 30 meters were overturned during attempts made to relocate them at 24 hour intervals. Twenty-five specimens of each of five additional species, Linckia guildingii, Linckia multifora, Nardoa novaecaledoniae, Nardoa pauciforis and Echinaster luzonicus, were released following similar tagging. Other methods of tagging, such as stains (Loosanoff, 1937; Feder, 1955; Vernon, 1937), were not successful because of low intensity of staining.

The feeding of starfish at Heron Reef was not examined in detail. When starfish specimens were collected, their stomachs were often found everted over the substrate. The approximate size of the stomach was noted along with the type of food material on which they appeared to be feeding. Any mark that their feeding activity may have left on the surface of the substrate was recorded.

3.3 Results

Culcita novaeguineae did not occur commonly in any habitat that was sampled by the shallow-water traverses. This species appeared to be more abundant in coral pools adjacent to the lagoon than on either the reef crest or reef flat at the western end of the reef. Linckia guildingii, Linckia laevigata, Nardoa novaecaledoniae and Nardoa pauciforis appeared to be slightly more abundant in one zone (primary habitat)

than another (secondary habitat), but this difference was not clear, and was not quantified. All the remaining species occurred with either much greater densities in their primary habitats compared with their densities in secondary habitats or were found in only one major zone.

The species that are regarded as exposed sometimes were found under boulders or coral rubble, but no regular pattern of concealment was apparent in these species. The cryptic species varied in their type of refuge, which ranged from small rubble to large boulders.

The primary (1′) habitat, secondary (2′) habitat and general pattern of concealment of each species are listed in Table 3.1. These data are not quantitative but represent a general impression of the overall distribution pattern for each species. While some species are extremely restricted in their spatial distribution, others are widespread and it was not possible to estimate the abundance of each species, in each zone, in each sampling period when specimens were primarily required for size-frequency and reproductive analysis.

The general location of each species at Heron Reef and the known diet of each of the species (after Yamaguchi, 1975 b) are listed in Table 3.2. While diet was not studied in detail, observations made during this study confirm those of Yamaguchi that most species of starfish feed on epibenthic felt.

Table 3.1 The species of Asteroidea, primary habitat, secondary habitat, and their habit (excluding those species that occur predominantly in the off-reef floor zone).

SPECIES	1′ HABITAT	2′ HABITAT	HABIT
Astropecten polyacanthus	floor	flat	exposed
Iconaster longimanus	slope	floor	exposed
Culcita novaeguineae	flat	crest, slope	exposed
Acanthaster planci	slope	flat	both
Asteropsis carinifera	crest		cryptic
Dactylosaster cylindricus	crest		cryptic
Fromia elegans	slope	crest	exposed
Fromia milleporella	crest		exposed
Gomophia egyptiaca	slope	crest	both
Linckia guildingii	flat	crest	exposed
Linckia laevigata	flat	crest	exposed
Linckia multifora	crest	slope	both
Nardoa novaecaledoniae	crest	flat	exposed
Nardoa pauciforis	flat	crest	exposed
Nardoa rosea	floor	flat	exposed
Neoferdina cumingi	slope	crest	both
Ophidiaster armatus	floor	crest	exposed
Ophidiaster confertus	crest		cryptic
Ophidiaster granifer	crest		cryptic

Ophidiaster lioderma	crest		cryptic
Ophidiaster robillardi	crest		cryptic
Ophidiaster watsoni	crest		cryptic
Anseropoda rosacea	flat		cryptic
Asterina anomala	crest		cryptic
Asterina burtoni	crest		cryptic
Disasterina abnormalis	crest		cryptic
Disasterina leptalacantha	flat	crest	cryptic
Tegulaster emburyi	crest		cryptic
Mithrodia clavigera	crest		exposed
Echinaster luzonicus	crest	flat, slope	both
Coscinasterias calamaria	crest		cryptic

Table 3.2

Diet and location of each species (excluding those species that occur predominantly in the off-reef floor zone). In some species the diet is unknown. asc = ascidian

SPECIES	DIET	LOCATION
Astropecten polyacanthus	mollusc	fine sand 0-30 m
Iconaster longimanus	felt	rubble 20-30 m
Culcita novaeguineae	coral, felt	sand, rubble 0-25 m
Acanthaster planci	coral	live coral 0-25 m
Asteropsis carinifera	-	sand under rock
Dactylosaster cylindricus	-	rock under rock
Fromia elegans	felt	rubble 0-25 m
Fromia milleporella	-	rubble
Gomophia egyptiaca	sponge, asc	sand, rubble 0-20 m
Linckia guildingii	felt	sand, rubble
Linckia laevigata	felt	sand, rubble
Linckia multifora	felt	attached under rock
Nardoa novaecaledoniae	felt	sand, rubble
Nardoa pauciforis	felt	sand, rubble
Nardoa rosea	-	sand, rubble 0-30 m
Neoferdina cumingi	-	sand, rubble 0-20 m
Ophidiaster armatus	-	sand, rubble 0-30 m
Ophidiaster confertus	-	rock under rock
Ophidiaster granifer	sponge, asc	attached under rock
Ophidiaster lioderma	-	rubble under rock
Ophidiaster robillardi	-	attached under rock
Ophidiaster watsoni		under boulder
Anseropoda rosacea		sand
Asterina anomala	sponge, asc	attached under rock
Asterina burtoni	sponge, asc	attached under rock
Disasterina abnormalis	felt	attached under rock
Disasterina leptalacantha	felt	attached under rock
Tegulaster emburyi	-	attached under rock
Mithrodia clavigera	-	rubble
Echinaster luzonicus	felt	sand, rubble 0-25 m
Coscinasterias calamaria	mollusc	attached under rock

In all species, excepting Acanthaster planci, the stomach was small, usually about the same area as the disc. At no time was the ingestion of large food material observed in any species but Astropecten polyacanthus and Coscinasterias calamaria were occasionally observed feeding on very small gastropods which were partially inside the mouth. In all other species the feeding was entirely extra-oral.

When the stomach was everted, the oral spines were oriented away from the mouth and both digestion and absorption occurred outside the body. At the completion of feeding, the stomach was withdrawn through the mouth and the oral spines were reoriented such that they occluded the mouth opening. All species commenced retraction of the stomach when removed from the substrate but the delay, before retraction was complete, varied from a few seconds in the case of

epibenthic felt feeders with small stomachs to a few minutes in the case of Acanthaster planci. In all species, the oral spines could not reorient into the non-feeding (defensive) positions until the stomach was fully retracted inside the mouth.

The only two species which left feeding scars on the substrate were Culcita novaeguineae and Acanthaster planci. Both of these species feed on hard coral. Culcita novaeguineae was observed also feeding on bryozoan colonies at the base of the reef slope at a depth of 20 meters. All the other species had not altered the appearance of the substrate on which they had been feeding. Fromia elegans, Linckia guildingii, Linckia laevigata, Linckia multifora, Nardoa novaecaledoniae, Nardoa pauciforis, Disasterina abnormalis, Disasterina leptalacantha and Echinaster luzonicus were only observed to evert their stomach over substrate of either sand or coral-rock that was covered with a fine layer of organic material (epibenthic felt). Ophidiaster granifer and Asterina burtoni were observed with their stomachs everted over both solitary and colonial ascidians, but these two species also everted their stomachs over the epibenthic felt.

The results of movement studies of Linckia laevigata showed that this species is capable of moving at least 30 meters in a 24 hour period. Only 12 out of 25 specimens, which were released on coral rubble substrate at the outer, northern reef flat were able to be relocated 24 hours later. Eight specimens had not moved, three specimens had moved one meter, one specimen had moved 15 meters, but 13 specimens had moved a distance greater than 30 meters and were not relocated. After a further 24 hours only two tagged specimens and no untagged specimens could be relocated in the vicinity of the point of release. Of the 25 specimens of six other species that were released following tagging, no tagged specimens were observed when attempts were made to relocate them after an interval of two months. It is possible that the small plastic tags were lost from the arms of these specimens.

3.4 Discussion

It can be seen from Table 3.1 that 16 of the 31 asteroid species recorded from Heron Reef were found in more than one of the major coral reef zones during this study. Echinaster luzonicus was found in all zones. The less common species were not encountered often enough for the data to show their complete distribution. With the exception of Culcita novaeguineae, Linckia guildingii, Linckia laevigata, Nardoa novaecaledoniae, Nardoa pauciforis and Echinaster luzonicus, the asteroids at or in the vicinity of Heron Reef can be divided into reef flat, reef crest, reef slope and off-reef floor species.

Species that occurred with their highest abundance on the reef flat are Culcita novaeguineae, Linckia guildingii, Linckia laevigata, Nardoa pauciforis and Disasterina leptalacantha. All species, excepting D. leptalacantha, are a large size when fully grown (large-bodied) and lie fully exposed in the daytime. However, they might complete their early development under boulders on the reef crest (Yamaguchi 1973 a, b). Disasterina leptalacantha is a small cryptic species found occasionally on the reef crest, or more often, under slabs of beachrock on the innermost part of the reef flat.

Linckia multifora, Nardoa novaecaledoniae and Echinaster luzonicus occurred with highest abundance on the reef crest. Species which were found exclusively on the reef crest are Asteropsis carinifera, Dactylosaster cylindricus, Fromia milleporella, Ophidiaster confertus, Ophidiaster granifer, Ophidiaster lioderma, Ophidiaster robillardi, Asterina anomala, Asterina burtoni, Disasterina abnormalis, Tegulaster emburyi, Mithrodia clavigera and Coscinasterias calamaria.

Predominantly reef slope species are Iconaster longimanus, Fromia elegans, Gomophia egyptiaca, Neoferdina cumingi and Acanthaster planci. Their distribution seems more closely allied to living coral than is that of the species which inhabit the reef flat or reef crest.

The off-reef floor is not a true coral reef environment although numerous solitary corals and alcyonarians occur. The asteroid fauna of this environment is made up chiefly of the widespread sub-littoral species Astropecten polyacanthus, Pentaceraster regulus and Euretaster insignis in the deeper water (30-40 meters). Nardoa rosea, Ophidiaster armatus, Tamaria megaloplax, Echinaster stereosomus and large individuals of Linckia multifora and Echinaster luzonicus are found in the shallower water (20-30 meters) near the base of the reef slope.

Of the 25 starfish species found on Heron Reef itself, 17 were located only in intertidal regions and an additional three were found predominantly in intertidal regions. The other five species have been found intertidally but occur predominantly in subtidal habitats.

Some cryptic reef crest species such as Asteropsis carinifera, Linckia multifora, Disasterina abnormalis, Echinaster luzonicus and Coscinasterias calamaria occur under rocks which possess a sparse development of epibiota. This would appear to be a short-lived micro-habitat. Other cryptic reef crest species such as Gomophia egyptiaca, Ophidiaster granifer, Ophidiaster robillardi, Asterina anomala and Asterina burtoni are more frequently associated with encrustations of sponges and ascidians (Yamaguchi, 1975 b). Ophidiaster confertus was found either under or attached to the side of large boulders on the reef crest. Other species such as Dactylosaster cylindricus, Neoferdina cumingi, Ophidiaster lioderma and Tegulaster emburyi were not located in sufficient numbers to establish any pattern of occurrence. The reef crest species, that are regarded as cryptic during the day, did not move into exposed locations at night and species could remain cryptic during periods of activity. The reef crest, interstitial environment, which is composed of highly fragmented coral, continually percolated by sea water, might provide refuges from desiccation and predation for some species but all attempts to locate asteroids in this micro-habitat were unsuccessful.

The epibenthic felt which covers large areas of intertidal coral reef habitat is composed primarily of protozoans, algae, and bacteria (Thomassin, 1976). At Heron Reef and on other reefs, this appears to be a substantial resource. It would be of interest to know if competitive exclusion of one or more species can occur when population densities are higher than those recorded at Heron Reef. The role of species-specific enzymes in the digestion of different organisms composing the epibenthic felt has not been investigated to date. Each species might possess enzymes which facilitate the efficient exploitation of a different component of the epibenthic felt. A biochemical study of the gastric mucosa of each asteroid species would be needed to establish resource partitioning on this microscopic scale.

The feeding and movements of Acanthaster planci was studied by Keesing and Lucas (1992). This species has been shown to possess an enzyme which can efficiently digest the wax ester, Cetyl Palmitate, which is stored in the soft tissues of hard corals (Benson et al., 1975; Brahimi-Horn, 1989). Consequently, this asteroid must be regarded as a highly specialised predator of scleractinians. It is possible that other

highly specialised enzymes occur in coral-reef asteroids. To exploit epibenthic felt efficiently, a scavenger would utilise mechanical or bacterial breakdown of algal cell walls and in other taxa this would be accomplished within a gut and the freed inter-cellular material would be subsequently assimilated by the organism. The epibenthic feeding asteroids evert their stomach over the felt and digestion occurs externally. These asteroids rely on enzymes to complete the digestion process but there are few known eucaryote enzymes which are capable of chemically digesting cellulose walls of algae. Diatoms, which are common in the epibenthic felt, have siliceous walls and the chemical digestion of this material, by any organism, would seem impossible. It is apparent, however, that many species of asteroid coexist on this same resource and further work is needed on possible dietary (enzyme) specialisation.

Predation on molluscs has been recorded in Astropecten polyacanthus and Coscinasterias calamaria. The paucity of mollusc-feeding coral-reef asteroids on Heron Reef is noticeable, compared with their high abundance in temperate waters (see Menge, 1975; Kwon and Cho, 1986; Nojima et al., 1986). Individuals of Coscinasterias calamaria found in the reef crest habitats were only small (R <20 mm), as were the gastropod prey on which they were observed feeding. The mobility of starfish might be insufficient to allow large-scale foraging on a coral reef as well as sufficient aggregation for successful reproduction.

Blake (1983) suggested that the general body plan of molluscivorous starfish leaves them vulnerable to predators. The observed delay in oral spine relocation following the commencement of stomach retraction, together with the defensive nature of these spines, suggests that the oral region of a starfish may be especially vulnerable to predatory attack particularly during and immediately following starfish feeding. The absence of adult specimens of Coscinasterias calamaria and other molluscivorous species of starfish may be related to the dangers inherent in this type of feeding.

In summary, the coral-reef starfish that occurred at Heron Reef showed some inter-specific variation with respect to diet, but many species appeared to feed on the same food (epibenthic felt). These species also showed some inter-specific variation with respect to habitat, but in every coral reef zone, some species sought no refuge and occurred with exposed habits. Of the species that occur predominantly on coral reefs, clear examples of niche (dietary or microhabitat) specialisation are known only for Culcita novaeguineae and the predominantly subtidal species Acanthaster planci. Clear

examples of competitive interactions were not observed during this study.

CHAPTER 4. POPULATION DENSITY

4.1 Introduction

It is well known that the scale of observation is critical for the determination of the spatial distribution pattern of a species. Differing scales of analysis can produce apparently differing results even with the same data. The properties or parameters that emerge from studies of communities can be dependent on which scale of organisation, space or time is chosen (Bradbury and Reichelt, 1982).

While the abundances of the various species of starfish will be partially determined by the small-scale distribution of scattered resources, the overall spatial distribution of each species will be a composite pattern influenced by food, refuge, and predator abundance as well as aggregation behaviour (Patton et al., 1991; Stevenson, 1992; Iwasaki, 1993). Each of these factors can vary at a number of scales.

For each species within this assemblage, population aggregation may vary either spatially (from one location to another) or temporally (over time at any one location). If there is an equal probability of locating a species at every point within its spatial distribution, then individuals of that species are distributed at random. However, if the geographical range of a species or its abundance variation within that range is attributed to either physical or biological parameters, then non-randomness of the spatial distribution of that species is directly implied.

If the scale of observation is such that individuals of a particular species would be expected to be distributed randomly throughout habitats, which themselves are distributed randomly in space, then the expected distribution of individuals in space will be clumped, not random. If low density populations of starfish are not expected to be distributed randomly, then density estimates can seriously underestimate the standard error of the mean. Failure to determine the degree of positive skewness in the density distribution results in poor repeatability. Population density estimates of non-random species are credible only when the extent of the positive tail of this distribution has been determined adequately.

4.2 Methods

Specimens were collected primarily for size-frequency and reproductive analysis. For logistical reasons, it was not possible to estimate the density of each species, in each zone, in each sampling period. For each species, the density on each traverse was calculated

by dividing the number of individuals by the estimated area of the traverse. The mean density of each species was then calculated by taking the arithmetic mean of the 72 traverse densities. It is represented as the average number of individuals found per hectare.

Because starfish are not distributed randomly, the total number of individuals of each species divided by the total area is not equal to the mean of the individual traverse densities. The standard deviation of density was calculated from the 72 traverse densities and represents the overall variation in density across all the traverses.

Because of the nature of traverse sampling, the density of most species is only approximate. Exposed species are reasonably well estimated, but the cryptic species are greatly underestimated in their abundance because not all coral rocks and boulders in each traverse were overturned. Although the under surface of rocks was examined closely, the nature of the substrate would make detection of the smaller species less reliable than the detection of larger species. When specimens were located within the sediment under rocks, individuals that were buried deeply within the rubble or sediment under these rocks would not have been found.

It should be noted that, in addition to patchiness, the number of individuals of each species recorded on different traverses varied because of variation in the size of traverse. The total number of each species also varied between sampling periods as a result of variation in the number of traverses undertaken in each sampling period.

Disasterina abnormalis was sampled in detail because it occurred in one region at a high density. This was the only species that could be sampled in this manner and this species appeared to occur at this density in only one region. The mean individual density per square meter, over a number of contiguous quadrats, and a Chi-square value (with Yates' correction) of the inter-quadrat variation was calculated for Disasterina abnormalis. Twenty (metre square) quadrats were laid at Site 1 in April 1980 and again in July 1980. Forty (metre square) quadrats were laid at Site 2 in April 1980. All specimens occurring within the quadrats were counted and measured. It is to be noted that this was a region of northern reef crest where the density of this particular species was known from traverse data to be high.

4.3 Results

The data presented in Table 4.1 show the densities of all the intertidal asteroid species that occurred within traverses during this study at

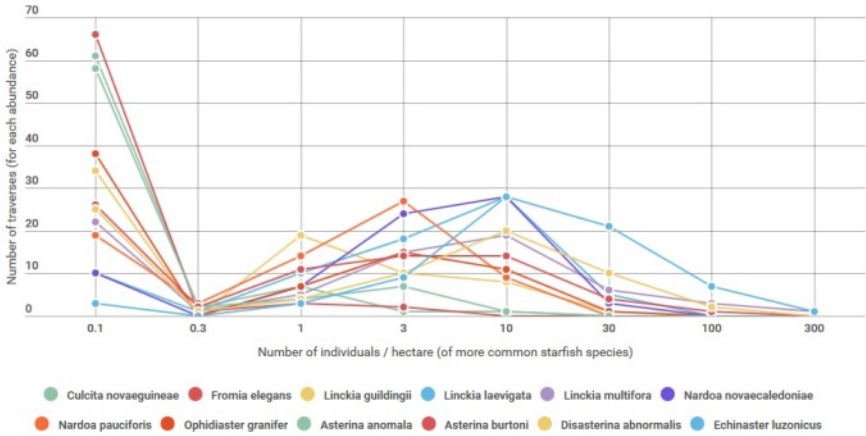
Heron Reef. For all species, the standard deviation was greater than the mean density. This, together with Figures 4.2 to 4.13, indicates variations in density that are greater than the expected Poisson variation. The results of quadrat density analysis of Disasterina abnormalis are shown in Table 4.2. The variation was analysed using chi square and individuals were clumped at the metre square scale.

Figure 4.1a graphs the linear relation between the total number of individuals and the total sample area. Figure 4.1b graphs the number of species in each of five (log) average density ranges. This illustrates how the average density of starfish species is distributed within this assemblage.

Figures 4.2 to 4.13 graph the population distribution of each of the common species, over the 72 traverses. Each graph displays the number of traverses on which a species occurred at a particular density. The density axis has been logged to facilitate the display of an extremely wide range of density.

Figures 4.14 and 4.15 are composite graphs of the population distributions of these species. Figure 4.14 graphs the population distributions of the six relatively abundant species, namely Echinaster luzonicus, Disasterina abnormalis, Asterina burtoni, Nardoa novaecaledoniae, Linckia multifora and Linckia laevigata. Figure 4.15 graphs the population distributions of the six less abundant species, namely Asterina anomala, Ophidiaster granifer, Nardoa pauciforis, Linckia guildingii, Culcita novaeguineae and Fromia elegans. The abundances of the 12 remaining species that occurred on traverses were very low and were not analysed.

Number of traverses : Number of individuals / hectare



From 1978 to 1984 on Heron and Wistari Reefs, most species of starfish are rare #CharoniaResearch

Table 4.1

The density of each species that occurred on intertidal traverses expressed as mean density (number per hectare), standard deviation (S.D.) and number (N) of individuals.

SPECIES	MEAN DENSITY	S.D.	N
Culcita novaeguineae	0.14	0.48	15
Asteropsis carinifera	0.02	0.12	3
Dactylosaster cylindricus	0.01	0.12	1
Fromia elegans	0.10	0.42	16
Fromia milleporella	0.002	0.01	1
Gomophia egyptiaca	0.12	0.57	6
Linckia guildingii	1.27	2.63	116
Linckia laevigata	4.01	4.87	509
Linckia multifora	7.51	17.30	522
Nardoa novaecaledoniae	3.19	3.72	326
Nardoa pauciforis	1.60	1.77	187
Nardoa rosea	0.002	0.01	1
Ophidiaster armatus	0.02	0.11	4
Ophidiaster confertus	0.03	0.15	4
Ophidiaster granifer	1.56	2.67	116
Ophidiaster lioderma	0.02	0.15	1
Ophidiaster robillardi	0.58	2.58	24
Asterina anomala	0.23	0.58	17
Asterina burtoni	3.27	6.99	208
Disasterina abnormalis	5.68	10.04	500
Disasterina leptalacantha	.23	1.31	7
Tegulaster emburyi	0.01	0.07	1
Echinaster luzonicus	16.16	24.67	1402
Coscinasterias calamaria	0.11	0.65	7

Table 4.2

Density and patchiness of Disasterina abnormalis.

The variation in number of individuals within adjacent square metre quadrats at two study sites and two sampling periods. DENSITY (the number of individuals per square metre), CHI-SQUARE (calculated from the inter-quadrat variation), PROB (the probability of this variation being random) and the NUMBER of individuals in the sample are tabled.

PERIOD	DENSITY	CHI-SQUARE	PROB.	NUMBER
APRIL 1980 SITE 1	8.4	58 (d.f.=24)	<.001	161
APRIL 1980 SITE 2	0.7		n/s	29
JULY 1980 SITE 1	8.9	11 (d.f.=11)	n/s	98

4.4 Discussion

The traverse data do not allow for a statistically valid comparison of density among different sites or different sampling periods. Four species of starfish appeared to demonstrate changes in density during the study period. Two of these species were capable of asexual reproduction and these species demonstrated periods of autotomy followed by periods of growth. These species were Linckia multifora and Echinaster luzonicus. Asexual reproduction following a sexual recruitment was suggested by Ottesen and Lucas (1982) and Yamaguchi and Lucas (1984) as the reason for the greatly different abundances of all asexually reproducing species at different places on the same reef.

The other two species that showed a large change in abundance were Disasterina abnormalis and Asterina burtoni. At the commencement of the sampling program, the density of Asterina burtoni appeared to be about half that of Disasterina abnormalis under boulders on the reef crest. The abundance change in Asterina burtoni could not be analysed accurately because Asterina burtoni did not occur in great abundance in any known habitat. As a result, it was not possible to sample its density using meter square quadrats. A temporal variation in the abundance of A. burtoni was recorded by Price (1981) in the Arabian Gulf. Disasterina abnormalis had periodic high recruitment with resultant changes in both its abundance and size-frequency distribution. For Linckia multifora, Echinaster luzonicus and Disasterina abnormalis, the changes in mean individual size results from periods of high recruitment which are discussed in the chapter on Population Stability. The range in abundance of Acanthaster planci in both outbreaking and non-outbreaking populations was investigated by Moran and De'ath (1992 a).

The results of quadrat sampling in an area of reef crest north of Heron cay where the density of Disasterina abnormalis was known to be high (Table 4.2, Site 1) showed an average density of 8.4 individuals per square metre. This region was the innermost part of the reef crest and was sheltered partially from heavy wave action by a bank of rubble which extended for about one kilometre. One hundred metres west of this rubble bank (Table 4.2, Site 2), in an otherwise similar region of the inner reef crest, the density of this species was less than one individual per square metre.

The number of individuals of Disasterina abnormalis per square metre showed too much variation in the April 1980 (Site 1) sample for the individuals to be randomly distributed at the time of sampling.

However, in the July 1980 (Site 1) sample, the individuals were not significantly clumped. It is of interest that the density per square metre of this species did not differ significantly between these two sampling periods. The only difference was in the degree of aggregation. Antonelli and Kazarinoff (1988) regarded the degree of aggregation of A. planci as an important factor in the modelling of population regulation by predators.

The quadrat samples produced only a minute subset of the known number of species, because such a small area was sampled. It was not feasible to sample extensively by quadrat as the patchy distribution of all these species required a large-scale estimate of spatial density variation.

Environmental heterogeneity might account for the observed clumping of individuals that were found primarily under boulders or rubble but does not explain the variation in abundance of exposed asteroids on traverses which crossed what appeared to be similar habitat. The effect of variation in physical parameters, such as depth of water, amount of siltation of substrate, and strength of wave action is unknown, and factors such as these might account for some of the observed differences in abundance.

It can be seen from Figures 4.2 to 4.13 that individuals of each of the species were usually either absent or reasonably well represented on traverses. Individuals of the more abundant species did not occur at higher densities on every traverse, but were located on more of the traverses and occurred more often at moderate and higher densities. Individuals of the less abundant species were absent from most of the traverses and occurred less often at the moderate densities and never at higher densities. The possibility of variation in the abundance of species from reef to reef also exists. This would be more noticeable if reefs maintain semi-closed circulations. The numbers of one species may gradually build up by local recruitment if larvae recruit to the parent population.

Some of the rarer species of coral-reef starfish are known only from their holotype or perhaps one or two paratypes and appear to exist at population densities which defy our normal understanding of population dynamics and reproductive strategies. It is not clear how these species survive and which, if any, ecological requirements or constraints limit their distribution or abundance. It is not known whether these species are rare because their necessary ecological requirements are met at only a small number of points or whether their rarity is a result of intense predation.

Recruitment involving survival to reproduction must occur at some points within the distribution of each species unless we are observing the process of extinction. Considering both the number of species involved and the fact that species such as Tosia queenslandensis, Ophidiaster lioderma and Tegulaster emburyi are considered rare throughout their geographical range, rare species must demonstrate physical or behavioural attributes which are adaptations to existence in low density populations. Levins and Culver (1971) suggested that specialised rare species might play a key role in ecosystem modulation, and they raised the possibility of specialised predation or competition among rare species.

Any assumption of a species abundance indicating its successfulness or adaptive nature should be questioned and the concept of species adapted to live in sparse populations offered as partial explanation of the high diversity in many ecosystems. The influence of specific predation can result in the rarity of a species and adaptations to this might represent a viable survival strategy (Connell, 1970). Spawning aggregations, extended gamete survival and high gamete specificity, hermaphroditism, parthenogenesis, and asexual reproduction are all ways of ensuring continuity of offspring in rare species. Certain very specialised species might occur only at a certain resource optimum, and their populations will be limited to the number of these sites of optimum habitat.

It is not known to what extent population fluctuations are normal on coral reefs. In the larger species of starfish at Heron Reef, the overall impression was that population fluctuations were low compared with the fluctuations that are known to occur on other reefs and in temperate ecosystems.

Because the abundance data resulting from the traverse samples was biased towards large, exposed individuals, it would be unwise to use this traverse data for a direct density comparison over repeated sampling periods. The non-randomness of the spatial distributions of these starfish populations, as evidenced by the large range in local density that was recorded in the populations of many of the species, further limits the validity of such a density comparison. For this reason, the variation in mean individual size was considered a more appropriate measure of change in the population structure of the species.

CHAPTER 5. SIZE STRUCTURE

5.1 Introduction

Many workers who have studied coral-reef asteroid populations have noted the adult-dominated size structure of these populations (Clark, 1921; Ebert, 1972; Yamaguchi, 1977 a). Similar findings have been made for asteroid populations from other communities (e.g. Paine, 1976). Although juvenile asteroids have been encountered on coral reefs, their abundance was so low and their appearance sufficiently different from that of the adults in some species, that juveniles have been placed in a species different from the adult (see Yamaguchi, 1975 b).

The population structure of some of the more common, large-bodied species of coral-reef asteroids such as Linckia laevigata has been studied (Yamaguchi, 1977 a; Laxton, 1974; Thompson and Thompson, 1982). In these studies, the size distributions of the asteroid were unimodal indicating either a large overlapping of generations or a dominant year class. If the latter alternative is true, the variation in growth rates within the population must be extraordinary to produce the observed size range. Most of the studies on Acanthaster planci occurring under non-outbreak conditions have shown a primarily adult population with small juveniles occurring only occasionally (Yamaguchi, 1973 a; Zann et al, 1987). In studies of large-bodied coral-reef asteroids, few individuals were found which were smaller than half the average size (Yamaguchi, 1973 a, 1973 b; 1977 a). In this chapter, the maximum size attained and the population structure of each of the commoner species constituting the asteroid fauna of Heron Island Reef will be investigated.

5.2 Methods

Specimens collected on traverses were allowed to resume an extended shape in a plastic bucket and were then measured using a plastic ruler. When animals were measured both the length from the mouth to the tip of the longest arm, and the average length from the mouth to the interradius were recorded to an accuracy of one millimetre. These are called major radius (R) and minor radius (r) respectively and are expressed in millimetres (mm). “R” was always measured along the ambulacral groove. After measurement, individuals were placed along with conspecifics in glass aquaria that were provided with fresh running sea water if they were needed for later experiments relating to their reproduction.

The major radius (R) is used as a measurement of overall size. The

ratio of major radius (R) to minor radius (r) is referred to as "R/r" or "R:r". Because it is a ratio it has no units. It is a measurement of the degree of arm elongation and is of taxonomic significance.

In addition to specimens collected on traverses at Heron Reef many sub-tidal specimens of Fromia elegans and specimens of Disasterina abnormalis found during the quadrat study were measured. This is the reason for the difference in sample size between the tables of abundance and mean size.

Juvenile asteroids of most common species were located under boulders on the reef crest. Their identification, although initially difficult, was always possible following microscopic examination and reference to earlier studies (Clark, 1921; Yamaguchi, 1975 a, 1975 b, 1977 a).

5.3 Results

Tables 5.1 – 5.10 summarise the mean size data of all individuals recorded in each sampling period for each of the common species. ANOVA tables showing the significance of variations of major radius (R) are included. Figures 5.1a – 5.10a graph the frequency distribution of major radius (R). Figures 5.1b – 5.10b graph the frequency distribution of major radius / minor radius (R/r). Figures 5.1c – 5.10c graph the relation between minor radius (r) and major radius (R). Figures 5.1d – 5.10d graph the relation between major radius / minor radius (R/r) and major radius (R). The relation between these two radii is variable, but it is frequently used as a taxonomic distinction. Minor radius (r) was not measured in August and November 1978 and these data are excluded from the ANOVA. Table 5.11 is a summary of the size data for each of the 24 species that occurred on intertidal traverses.

Juveniles of Fromia elegans, Linckia laevigata, Nardoa novaecaledoniae and Nardoa pauciforis occurred rarely. The size-frequency distributions of major arm radius (R) show clearly the paucity of small individuals (R less than half the mean R) in the populations of these species. Linckia guildingii, Linckia multifora, Ophidiaster robillardi, Asterina anomala, Echinaster luzonicus and Coscinasterias calamaria reproduce asexually. Small individuals of these species, resulting from autotomy or fission, occurred intermittently throughout the period of the study . Juveniles of Asterina burtoni and Disasterina abnormalis occurred throughout the period of the study. The size- frequency distributions of major arm radius (R) show the abundance of small individuals in these species.

Ophidiaster granifer was not common, but its highly skewed size-frequency distribution shows the presence of medium sized individuals (R half the mean R). With the exception of one specimen each of Culcita novaeguineae (R=50 mm) and Gomophia egyptiaca (R=10 mm), juveniles of less common species did not occur.

Table 5.11

The mean major radius (MEAN R mm), mean major radius / minor radius (MEAN R/r) and sample size (N) of the species that occurred on traverses at Heron Reef.

SPECIES	MEAN R mm	MEAN R/r	N
Culcita novaeguineae	109	1.3	12
Asteropsis carinifera	74	2.8	3
Dactylosaster cylindricus	83	-	1
Fromia elegans	32	3.9	183
Fromia milleporella	30	2.3	1
Gomophia egyptiaca	45	4.8	10
Linckia guildingii	134	9.8	131
Linckia laevigata	127	6.5	516
Linckia multifora	38	7.3	396
Nardoa novaecaledoniae	88	5.7	361
Nardoa pauciforis	104	6.6	233
Nardoa rosea	88	6.2	7
Ophidiaster armatus	55	6.3	7
Ophidiaster confertus	86	8.2	4
Ophidiaster granifer	27	4.3	121
Ophidiaster lioderma	105	-	1
Ophidiaster robillardi	37	6.9	21
Asterina anomala	4	1.6	16
Asterina burtoni	13	1.8	203
Disasterina abnormalis	15	1.9	1109
Disasterina leptalacantha	13	2.0	8
Tegulaster emburyi	18	2.3	1
Echinaster luzonicus	48	5.8	988
Coscinasterias calamaria	19	4.4	8

5.4 Discussion

The species of starfish that occurred on the traverses can be grouped according to general body size. The species that had a maximum major radius (R) greater than 100 mm were regarded as large-bodied. The large-bodied species (maximum major radius in parenthesis) are Culcita novaeguineae (130 mm), Linckia guildingii (240 mm), Linckia laevigata (190 mm), Nardoa novaecaledoniae (115 mm), Nardoa pauciforis (135 mm), Nardoa rosea (101 mm), Ophidiaster confertus (102 mm) and Ophidiaster lioderma (105 mm).

Small-bodied species had a maximum major radius (R) that was less than 100mm. These species were Asteropsis carinifera (85 mm), Dactylosaster cylindricus (83 mm), Fromia elegans (46 mm), Fromia milleporella (30 mm), Gomophia egyptiaca (64 mm), Linckia multifora (90 mm), Ophidiaster armatus (73 mm), Ophidiaster granifer (48 mm), Ophidiaster robillardi (50 mm), Asterina anomala (7 mm), Asterina burtoni (23 mm), Disasterina abnormalis (27 mm), Disasterina leptalacantha (20 mm), Tegulaster emburyi (18 mm), Echinaster luzonicus (100 mm) and Coscinasterias calamaria (30 mm).

With the exception of Ophidiaster confertus and Ophidiaster lioderma, large-bodied species possessed an extremely tough body wall. Ophidiaster confertus is a temperate species and Ophidiaster lioderma (an extremely rare species) is covered with a greatly thickened skin. The cut-off distinguishing large-bodied from small-bodied starfish at maximum R = 100 mm is arbitrary, and both Asteropsis carinifera and Dactylosaster cylindricus could be included in this large-bodied group if the distinction was based on mean size. The mean size of the two next largest small-bodied species, Linckia multifora and Echinaster luzonicus, remained about half the maximum size through a continuing process of autotomy.

It can be seen from the data presented in Tables 5.1 to 5.11 and Figures 5.1a to 5.10a that juveniles of the relatively common, sexually reproducing, large-bodied asteroids, Linckia laevigata, Nardoa novaecaledoniae and Nardoa pauciforis were rare and the populations of these species were adult dominated throughout the study period. Relatively small specimens of Linckia guildingii resulting from asexual reproduction were observed but these individuals represent only a minor component of the adult dominated population. In all large bodied species, distinct year classes were not observed in the population size structures. While a highly variable growth rate can disguise a dominant year class, the fact that neither numerous small individuals (indicating high recruitment) nor obvious population

declines (evidence of high mortality) were observed over a period of several years, suggests strongly that these species are long-lived (persistent).

Small individuals were more common in the populations of Linckia multifora, Echinaster luzonicus and Disasterina abnormalis, and to a lesser extent in the populations of Ophidiaster granifer and Asterina burtoni. These juveniles resulted from either sexual or asexual reproduction. While small specimens occurred in the sub-tidal population of Fromia elegans, its population structure was still adult dominated throughout the period of study.

Many hypotheses have been proposed to explain the apparent paucity of juveniles amongst coral-reef echinoderms. Juveniles may occupy such different habitats from the adults that they have not been adequately sampled or the adult animals may be long lived and recruitment low (Yamaguchi, 1977 a). Recruitment may also be patchy in both time and space (Yamaguchi, 1973 a, 1973 b, 1977 b). In studies of some fishes, it has been shown that each reproductive season large quantities of sperm and eggs are released but owing to the rigours of planktonic life and the uncertainty of locating settling substrate, most larvae are lost before settlement (Sale, 1976, 1977). Endean and Cameron (1990 b) proposed that the mortality that regulates the adult population density of Acanthaster planci occurs on post-settlement stages.

The giant triton (Charonia tritonis) and other members of the genus Charonia are known predators of many species of starfish (Chesher, 1969 b; Endean, 1969; Laxton, 1971; Noguchi et al., 1982; Percharde, 1972) and other predators of starfish include shrimp (Glynn, 1974), a worm (Glynn, 1984), fish (Ormond et al., 1973) and other starfish (Mauzey et al, 1968; Dayton et al, 1977; Birkeland et al, 1982). In most species at Heron Island, evidence of starfish mortality was hard to find. This has also been true for Acanthaster planci, even following population outbreaks. A high incidence of sub-lethal predation on adult Acanthaster planci was reported by McCallum et al. (1989), who suggested that lethal predation could account for the paucity of juveniles in populations of Acanthaster planci.

Parasitism of starfish by molluscs is well known (see e.g. Davis, 1967; Elder, 1979; Egloff et al., 1988). At Heron Reef, the incidence of infection by molluscs was low, except in Linckia multifora and Ophidiaster granifer. Bouillon and Jangoux (1985) recorded a high proportion of Linckia laevigata infected, but a high rate of infection of this species did not occur at Heron Reef.

Yamaguchi (1977 a) showed a much higher abundance of Linckia laevigata at Guam (a reef known to carry A. planci outbreaks) but the mean individual size was much smaller than in the present study. Thompson and Thompson (1982) and Laxton (1974) also found a smaller mean size of Linckia laevigata compared with that found in this study. Thompson and Thompson's study was conducted at Lizard Island, Queensland (a reef known to carry A. planci outbreaks) and a greater spatial variation in density and mean size was found than was evident at Heron Reef. While Laxton's samples were taken from Heron Reef in approximately the same habitat as was used in this study, the abundance of Linckia laevigata is not stated and there appears to have been confusion with Linckia multifora. Observations made at Lady Musgrave Reef in the Bunker Group where Linckia laevigata was much more abundant than at Heron Reef also show a smaller mean size of specimens from some habitats. Lady Musgrave Reef is known to have carried a minor outbreak of Acanthaster planci. The data indicate that abundance and mean individual size may be inversely correlated, but abundance appears to be more closely regulated on a reef such as Heron Reef that is not known to have carried an A. planci outbreak. Apart from the destruction of the hard coral cover caused by such outbreaks, great changes occur in the fauna and flora of reefs following A. planci population outbreaks (Endean and Cameron, 1990 b).

CHAPTER 6. SEXUAL REPRODUCTION

6.1 Introduction

Most asteroids possess 10 gonads, two in each ray with gonoducts opening in the interradii. In some coral-reef genera, such as Linckia and Nardoa, the gonads are arranged serially with numerous gonoducts existing along the length of the arm. When an individual is ready to spawn, the gonads can occupy the whole length of a ray. In most species, the sexes are separate, but hermaphroditism has been reported in Asterina burtoni (Achituv, 1972; Achituv and Malik, 1985; Achituv and Sher, 1991). In all coral-reef species studied previously, fertilisation is external with gametes being released directly into the water. An off-reef species, Euretaster insignis, belongs to the family Pterasteridae, other members of which are known to brood their young within the supra-dorsal membrane (McClary and Mladenov, 1989; McClary, 1990). The spawning of one individual might trigger other individuals to spawn, thus increasing the chance of fertilisation (Okaji, 1991). Alternately, synchronous spawning might be triggered extrinsically (see Yamaguchi and Lucas, 1984; Minchin, 1987).

The sexual reproductive cycle has been studied in some of the commoner coral-reef species e.g. Asterina burtoni, (by Achituv, 1972; James, 1972; Achituv and Malik, 1985), Linckia laevigata (by Yamaguchi, 1977 a), and Ophidiaster granifer (by Yamaguchi and Lucas, 1984). The type of larval development has also been studied in several species e.g. Astropecten polyacanthus (by Oguro et al., 1975), Acanthaster planci (by e.g. Henderson and Lucas, 1971), Gomophia egyptiaca (by Yamaguchi, 1974), Leiaster leachi (by Komatsu, 1973), Ophidiaster granifer, Ophidiaster robillardi and Ophidiaster squamous (by Yamaguchi and Lucas, 1984). The known forms of reproduction along with the type of larval development of most Guam species are tabled by Yamaguchi (1975 b).

The use of the hormone 1-methyl adenine to produce final maturation and subsequent release of gametes in asteroids is well documented (Kanatani, 1969, 1973). Yamaguchi (1977 a) described the injection of the hormone into the coelomic cavity of Linckia laevigata to assess the stage of development of the gonads. This procedure was also used by Yamaguchi and Lucas (1984). The presence and strength of response to treatment have been shown to depend upon the stage of maturation of the gametocytes (Kuborta et al., 1977).

The time required before a response is produced, following treatment,

depends upon the proximity of the natural breeding season (Kanatani, 1969). A delayed response in the genus Echinaster was described previously by Turner (1976). Additionally, it is possible that not all individuals within a population are at exactly the same stage of gamete development at any time (see Pearse, 1968).

6.2 Methods

The reproductive analysis of each of the species entailed the injection of 1-methyl adenine into the arms of a sample of the population several times during each year. The chemical was obtained as anhydrous powder in 10 mg tubes from Sigma Chemicals. The anhydrous powder was kept frozen following delivery. The concentration of 1-methyl adenine used for injection was 0.0001 M. dissolved in seawater. A working solution was prepared freshly for each sampling period and stored in a refrigerator at 4°C. It was necessary to warm the seawater temporarily to 40°C to facilitate the dissolution of the chemical as the working solution was being prepared. Once the chemical was dissolved (requiring about five to ten minutes with stirring) it was immediately placed in the refrigerator. The solution was not warmed again before injection into the starfish.

The quantity injected per individual depended on the mean size of the species tested. It ranged from one millilitre per individual in small species such as Ophidiaster granifer to five millilitres per individual in large species such as Linckia laevigata. In large species, the hormone was injected into three of the arms of each animal while it was temporally removed from the aquarium. In smaller species the injection was administered aborally into one interradius. Following injection, each animal was returned to its aquarium along with other conspecifics which had also been injected. The test animals were then observed for several hours and any release of gametes through the gonopores was recorded. To maintain visibility within the test aquaria, specimens were removed and placed in a larger tank once they commenced spawning. Spawning always continued following the transfer. Gametes that were fertilised in aquaria were never released in the field.

The procedure used by Kanatani (1969) required the extraction of gonad for in vitro treatment with 1-methyl adenine. Other methods of determining reproductive periodicity, such as gonad index or histological examination require the test individuals to be killed, and the gonads removed. Many species of coral-reef asteroid occur in low abundance and the regular killing of test individuals would have required the use of much smaller sample sizes to ensure that the

population was not reduced by periodic testing. In the present study the convenience of an in vivo treatment, that allowed the rapid testing of a large number of individuals of each species, was considered to outweigh the limitations imposed by the lack of detailed histological information.

Possible variability in response within samples required sample sizes in the vicinity of 20 to 30 individuals to ensure statistical significance of the different spawning frequencies, at different times of the year. Histological study would have provided direct qualitative evidence of gametogenesis. The dichotomous (presence / absence) spawning data obtained in the present study required larger sample sizes to demonstrate any periodicity conclusively. The G Test was used to establish that the observed response in the breeding season was significantly different from the null (low all year round) response. While in some cases, the "expecteds" were as low as two, the G statistic appeared sufficiently high to indicate a significant spawning response.

6.3 Results

Release of gametes required no longer than 3 hours after injection except in Echinaster luzonicus. However, for every species that was studied, the response time varied throughout the year. This time ranged from just under three hours, two months before the breeding season, to as little as 15 minutes at the peak of the season. At this peak, if the water temperature within aquaria was allowed to rise above that of the reef flat (as it would on a very hot day), spontaneous spawning was observed in species of Linckia and Nardoa. Spawning in the field was not observed during this study. The result with 1-methyl adenine was always reduced if the test animals had undergone previous spawning.

Tables 6.1a to 6.8a list the spawning response to injection with 1-methyl adenine and Figures 6.1 to 6.8 graph the annual spawning pattern of each of the common species over the study period. Tables 6.1b to 6.8b show the results of the G test, comparing the spawning response in four seasons. Table 6.9 lists the reproductive strategies of each species.

Providing that the water did not become too cloudy, it was always possible to determine the sex of the individuals by the type of gamete released. The size, number and development of eggs was not studied in detail but varied among species depending on the type of larvae produced.

The results of observations, relating to 1-methyl adenine injections, on the sexual reproductive cycles of the commoner asteroid species at Heron Reef are outlined below.

Females of Fromia elegans release from 100 to 200 very large (approximately 2.0 mm diameter) eggs from gonopores, two of which are located in each interradius. The eggs are bright red in colour and are of neutral buoyancy. Egg release may take up to three hours following injection but can occur after only 30 minutes. The males spawn within one hour and sperm are released through gonopores which are located slightly higher in each interradius than in the female. The fertilised eggs undergo lecithotrophic development. The peak of sexual activity occurred in early summer (November, December).

Females of Linckia guildingii release large numbers of small (approximately 0.1 mm diameter), colourless and negatively buoyant eggs through gonopores located serially along the arms. At no time was the sexually active proportion of the population very high. The peak in sexual activity that was apparent occurred in mid-summer (December).

The reproductive cycle of Linckia laevigata, at Guam, was studied by Yamaguchi (1977 a). Females release very large numbers of small (approximately 0.1 mm diameter), colourless and negatively buoyant eggs through gonopores located serially along the arms. At Heron Reef, L. laevigata showed a positive response to treatment (approximately 1 million eggs shed) from mid-winter to mid-summer. Spontaneous spawning occurred only in the summer months (November, December).

Females of Nardoa novaecaledoniae release approximately 1000, large (approximately 1.0 mm diameter), orange and positively buoyant eggs from gonopores arranged serially in each arm. The eggs undergo lecithotrophic development. The peak of sexual activity occurred in late summer (January) but specimens dissected in mid-winter (July) showed extensive gonad development. No response to 1-methyl adenine injection could be produced at this time. It would appear that this species can spawn and undergo complete gametogenesis within six months, but spawning was observed only once a year.

Females of Nardoa pauciforis produce eggs which appear very similar to that of Nardoa novaecaledoniae. They are the two common species of this genus on the Great Barrier Reef and are both very similar as adults. They are distinguished by the compression of the distal plates

of the arms in Nardoa novaecaledoniae. The peak of sexual activity occurred one month earlier (December) in Nardoa pauciforis than in Nardoa novaecaledoniae, indicating a degree of reproductive isolation in these species at the southern end of the Great Barrier Reef.

Ophidiaster granifer produces eggs which undergo parthenogenetic development (Yamaguchi and Lucas, 1984) and in this study only females (total of 7 individuals) were observed to spawn. Small numbers (20-60 per female) of large (0.6 mm diameter), neutrally buoyant, bright red eggs underwent at least initial development despite no obvious sperm having been released in the water. The only spawning activity in this species was observed in early summer (November, December).

Disasterina abnormalis does not appear to be abundant on the Great Barrier Reef other than in the Capricorn Group at its southern end. At Heron Island this species is abundant behind an extensive rubble bank on the northern side of the reef. The eggs of this species are small (approximately 0.1 mm diameter), colourless and sticky. They sank to the bottom of the aquarium and adhered to the glass, from which they were hard to dislodge. The type of development is unknown. The peak of sexual activity occurred in late spring (October).

Echinaster luzonicus liberates small numbers (20-100 per female) of positively buoyant and approximately 1.0 mm in diameter red eggs during late summer (February). Specimens with fully developed arms were selected for the injection of hormone as arm regeneration following autotomy, which is common in this species, may be at the expense of gonad development.

The remaining species either showed no response to 1-methyl adenine or were not sampled in sufficient numbers to establish reproductive periodicity. The following responses to treatment occurred:

Iconaster longimanus no response July (N=1)

Culcita novaeguineae one female Feb (N=4) no response Oct (N=4)

Asteropsis carinifera no response July (N=1)

Gomophia egyptiaca two males and one female Dec (N=3) no response Feb (N=1), May (N=1), July (N=2)

Linckia multifora no response throughout study (N=120)

Nardoa rosea one male Feb (N=1) no response July (N=2), Nov (N=4)

Ophidiaster armatus one male July (N=2) no response Feb (N=1), Oct (N=1), Dec (N=1)

Ophidiaster confertus no response July (N=1)

Ophidiaster robillardi no response May (N=7), June (N=1), Oct (N=4), Nov (N=1), Dec (N=3)

Tamaria megaloplax no response July (N=1)

Asterina burtoni no response throughout study (N=59)

Echinaster stereosomus no response July (N=2)

Table 6.9 The primary type of reproduction (REPRO) and the type of larval development (DEVEL) where known are shown for all asteroid species recorded from Heron Reef.

– = not known; PLANK = Planktotrophic; LECITH = Lecithotrophic; A = Achituv (1972); B = Barker (1977); Y = Yamaguchi (1975); * = this study

SPECIES	REPRO.	DEVEL.	SOURCE
Astropecten polyacanthus	SEXUAL	PLANK	Y
Iconaster longimanus	-	-	
Culcita novaeguineae	SEXUAL	PLANK	Y
Acanthaster planci	SEXUAL	PLANK	Y
Asteropsis carinifera	SEXUAL	PLANK	Y
Dactylosaster cylindricus	-	-	
Fromia elegans	SEXUAL	LECITH	*
Fromia milleporella	-	-	
Gomophia egyptiaca	SEXUAL	LECITH	Y
Linckia guildingii	ASEXUAL	PLANK	*
Linckia laevigata	SEXUAL	PLANK	Y
Linckia multifora	ASEXUAL	PLANK	Y
Nardoa novaecaledoniae	SEXUAL	LECITH	*
Nardoa pauciforis	SEXUAL	LECITH	*
Nardoa rosea	SEXUAL	LECITH	*
Neoferdina cumingi	-	-	
Ophidiaster armatus	-	-	
Ophidiaster confertus	-	-	
Ophidiaster granifer	SEXUAL	LECITH	Y
Ophidiaster lioderma	-	-	
Ophidiaster robillardi	ASEXUAL	-	
Ophidiaster watsoni	-	-	
Anseropoda rosacea	-	-	
Asterina anomala	ASEXUAL	-	A
Asterina burtoni	SEXUAL	-	A
Disasterina abnormalis	SEXUAL	-	*
Disasterina leptalacantha	-	-	
Tegulaster emburyi	-	-	
Mithrodia clavigera	SEXUAL	PLANK	Y
Echinaster luzonicus	ASEXUAL	LECITH	*
Coscinasterias calamaria	ASEXUAL	PLANK	B

6.4 Discussion

The species of coral-reef asteroids studied at Heron Island showed differences in the length of their breeding season and this may reflect on their colonisation ability (Mileikovsky, 1971). The length of the breeding season within a species might vary with latitude and the further the population is from the equator, the shorter may be the season for summer breeders. However, except for Linckia laevigata, the species studied at Heron Reef generally showed a one to two month breeding season. In two species, Linckia multifora and Asterina burtoni, no sexual activity was observed throughout the study. This might result from lower than required water temperature at Heron Reef for most of the year (see Mladenov et al., 1986). In this regard, Mortensen (1937) was able to obtain eggs from Linckia multifora in the Red Sea where the water temperature is higher than at Heron Reef. It might also be correlated with an increased emphasis on asexual reproduction in Linckia multifora once a reef has been colonised by a few sexually reproduced individuals. Although Asterina burtoni was not observed to undergo either sexual or asexual reproduction, the distinction between A. burtoni and the small fissiparous A. anomala is unclear. It is possible that A. anomala is an asexually reproducing form of A. burtoni.

Nardoa novaecaledoniae and N. pauciforis possess arms swollen with gametes for much of the year but still have only a limited breeding season. At Heron Reef, at the southern end of the Great Barrier Reef, Nardoa pauciforis is reproductively mature earlier in the summer than is Nardoa novaecaledoniae and its eggs are released in November or early December. At this time Nardoa novaecaledoniae is not capable of releasing eggs and sperm. Although both species look similar they appear to have limited interbreeding, at least over part of their geographic range. In general, temperature seems to be an important factor in gametogenesis, but the final spawning trigger is dependent on lunar/tidal cycles in many species (Pearse, 1970, 1975; Yamaguchi and Lucas, 1984).

In coral-reef asteroids the range in fecundity is extremely large. Fromia elegans, Gomophia egyptiaca, all species of Nardoa, Ophidiaster granifer and Echinaster luzonicus produce large, buoyant, highly pigmented, and yolky eggs. While larval development was not studied in detail, the initial phases of lecithotrophic development were observed in these species. The large reserves of yolk should ensure that the resulting larvae need not feed while in the plankton. The number of eggs produced with this development was not studied in detail but appeared to be relatively small (that is, less than 1000 and

sometimes much fewer per individual). The eggs are buoyant, opaque and 0.6 to 2.0 mm in diameter. For any species, the egg size, in combination with number of eggs liberated, is an index of reproductive effort. The energetic fecundity in relation to body size of different species, might represent qualitatively different reproductive strategies.

Planktotrophic larvae are produced by Astropecten polyacanthus, Choriaster granulatus, Culcita novaeguineae, Acanthaster planci, Asteropsis carinifera, all species of Linckia, Mithrodia clavigera, Leiaster leachi and Coscinasterias calamaria (Yamaguchi, 1975; Barker, 1977). With this type of larval development, many (up to 1 million), small (0.1 to 0.2 mm), non-yolky, transparent eggs are produced. These eggs appeared less buoyant than eggs that contain large yolk reserves. This may influence dispersion.

Larvae of species of Nardoa and other genera which undergo lecithotrophic development may be less likely to die of starvation in the plankton compared with those of species that undergo planktotrophic development and have an obligate larval feeding stage before settlement (see e.g. Thorson, 1950, 1966; Vance, 1973; Barker, 1977; Strathmann and Vedder, 1977; McEdwards and Janies, 1993). Lecithotrophic larvae have shorter development times, but the planktonic stage can be extended if suitable settlement sites are not available (Strathmann, 1978; Yamaguchi, 1974; Yamaguchi and Lucas, 1984). However, these larvae cannot remain in the plankton for as long as larvae with planktotrophic development. Their dispersal ability and genetic exchange is lower (Scheltema, 1968, 1971; Nishida and Lucas, 1988; Nash et al., 1988; Mladenov and Emson, 1990; Benzie and Stoddart, 1992 a,b). Yamaguchi (1975 b) has commented on the low abundance of lecithotrophic species on oceanic atolls. However, such species are well represented at Heron Reef, a situation that might result from the proximity of adjacent reefs, which would allow short lived larvae from one reef to settle on nearby reefs (see Fisk and Harriott, 1990). Any species may have difficulty colonising over distances greater than its larval dispersal capacity and lecithotrophic species might suffer local extinction following large scale destruction or alteration of coral reef habitat.

Despite the high sexual reproductive effort displayed by most of the large-bodied species, there is little evidence of high recruitment of starfish at Heron Reef. Loosanoff (1964) observed periodic high recruitment during a 25 year study of the temperate species Asterias forbesi. Periodic high recruitment has also been observed in the coral

reef species Acanthaster planci.

It is possible that many eggs are never fertilised when adult populations exist at low densities, such as at Heron Reef. Many fertilised eggs or subsequent larvae would also die from predation or starvation in the plankton (Jackson and Strathmann, 1981; Olsen, 1987). The availability of suitable settling substrate or post-settlement benthic predation might also limit the recruitment of juveniles.

It might be expected that planktonic regulation would be less constant than benthic regulation because of the relative unpredictability of small scale water circulation and the extremely patchy distribution of planktonic predators compared with a possibly more regular and species-specific mortality caused by benthic predators. The post-settlement survival of small juvenile Acanthaster planci was examined by Keesing and Halford (1992) and Keesing and Cartwright (1993) who found a difference in survivorship between caged specimens compared with uncaged specimens. For the less common species at Heron Reef, it is possible that many of their eggs are not fertilised. Adult numbers will be further regulated by a combination of either larval starvation or larval and juvenile mortality.

When the energy content of a liberated egg is considered, two different reproductive strategies are apparent. Sexual recruitment can follow either planktotrophic or lecithotrophic larval development (Hendler, 1975; Yamaguchi, 1977 b; Lessios, 1990; McEdwards and Chia, 1991). Because many small eggs can represent the same investment of energy as a few large eggs, the energetic fecundity per unit body weight can be similar in both strategies, despite the difference in numerical fecundity.

It has been suggested (Vance, 1973; Yamaguchi, 1973 a, 1973 b, 1977 b) that lecithotrophic development is an adaptation to high predation or starvation of larva. With this development it is possible the length of larval life can be shorter and hence larval survival should be favoured. On oceanic atolls, species with lecithotrophic development are never abundant and this could result from their poor dispersal ability (Yamaguchi, 1975 b). On Heron Reef, and possibly the Great Barrier Reef in general, where many reefs exist in relatively close proximity, lecithotrophic genera such as Nardoa, Fromia and Echinaster appear to be more abundant than they are on atolls. However, planktotrophic development is favoured where high dispersal is required or when planktonic predation is low and planktonic food is predictable (Menge, 1975; Mileikovsky, 1971; Vance, 1973; Yamaguchi, 1977 b). Many species with this type of larval

development occur on oceanic atolls but they occur also on the reefs of the Great Barrier Reef.

Disasterina abnormalis liberated small sticky eggs which sank and adhered to the substrate. The type of development was not studied, but the low dispersion capacity of its eggs might explain its apparently limited distribution. This species was abundant locally. In all other sexually reproducing species, juveniles were uncommon and there was no evidence of either periodic high recruitment or mortality.

The extent of larval dispersion is an important factor in our understanding of the community dynamics within a reef or reef system. If high between-reef larval dispersal occurs, then the adaptive significance of the dispersal phase is the location of spatially and temporally isolated patches in the survival mosaic of each species. Alternately, if larvae recruit primarily into the parent reef population, as a result of circular water movement patterns (Atkinson, Smith and Stroup, 1982; Dight et al., 1990 a, b; Black and Moran, 1991; Black, 1993 but see Wolanski, 1993), then the adaptive significance of the dispersal phase is the avoidance of planktonic or benthic predation in shallow water.

The development time of one month, possessed by many asteroid larvae with planktotrophic development (Yamaguchi, 1977 b; Williams and Benzie, 1993), allows potentially high dispersal, and this development time can be extended further if no suitable settlement site is available. Larvae with lecithotrophic development are capable also of extending the length of the pelagic phase (Yamaguchi, 1974; Yamaguchi and Lucas, 1984). The larvae of coral-reef starfish generally require a solid substrate to complete their development, and a coralline algal substrate has been observed as the chosen settling surface for many species (Yamaguchi, 1973 b; Johnson et al., 1991). More complex species-specific signals, located by sensitive chemosensory receptors might ensure settlement in habitats which are conducive to survival of post-settlement stages (Burkenroad, 1957; Morse, 1984). Yamaguchi (1977 c) showed that some juvenile starfish have exponential growth during the period following settlement and proposed that juveniles are subject to high mortality during this period. The juveniles transform to adult morphology at a certain size and before this size is attained may look quite different from adults (e.g. Culcita novaeguineae illustrated by Clark, 1921).

The phenomenon of aggregation (Ormond et al., 1973), parthenogenetic development (Yamaguchi and Lucas, 1984), hermaphroditism (Achituv, 1972) or asexual reproduction (Rideout,

1978) may be correlated with survival at low population densities. In low density, spatially dispersed populations of starfish, there is a low probability of locating a conspecific of the opposite sex at breeding time.

CHAPTER 7. ASEXUAL REPRODUCTION

7.1 Introduction

Some species of coral reef Asteroidea are known to exhibit both sexual and asexual reproduction (Yamaguchi, 1975b). The species known to reproduce asexually are detailed by Emson and Wilkie (1980). Rideout (1978) has shown that asexual reproduction is the chief form of reproduction in the asteroid Linckia multifora at Guam. The relative roles of sexual and asexual reproduction in the population maintenance of other coral reef asteroid species has not been studied. It is not known whether the asexually-reproducing species have a regular alternation of sexual and asexual activity, or if sexual reproduction is strongly reduced or even absent in any of these species.

In asteroids, asexual reproduction involves either the splitting of the disc (fission), or the casting off of arms that regenerate new starfish (autotomy). In some species, autotomized arms need not contain any section of disc or madreporite for their survival (Clark, 1913; Edmondson, 1935). The regeneration of a mouth and basic digestive organs must occur while the regenerating arm is metabolizing stored reserves of energy. A description of the stages of regeneration, following autotomy in Linckia multifora, is provided by Rideout (1978). This period of regeneration following autotomy, before the regenerated arms are ready for re-autotomy, might be prolonged greatly in species larger than Linckia multifora. Autotomy is reduced when individuals are infected with the parasitic gastropod Stylifer as this parasite inhibits autotomy of infected arms. Because the mortality of regenerating individuals is high (Davis, 1967; Rideout, 1978), though not as great as expected by Clark (1913), this inhibition of autotomy results in greater survival of the parasite (Davis, 1967).

An alternation of sexual and asexual activity has been observed in Nepanthia belcheri (Ottesen and Lucas, 1982). Some sexual activity has been recorded in the asexually reproducing species, Ophidiaster robillardi (Yamaguchi and Lucas, 1984). Other species, such as Asterina anomala and Linckia multifora, often remain small and sexually immature through the continuing process of asexual autotomy or fission. Some sexual activity has been noticed in Linckia multifora and Linckia guildingii (Mortensen, 1937, 1938) but the contribution of this may be outweighed by that of autotomy as a means of population maintenance (Rideout, 1978).

Asexual reproduction can avoid intense benthic and planktonic larval predation, as well as the general vicissitudes of planktonic life which include dispersal loss and starvation (see Ottesen and Lucas, 1982; Rideout, 1978; Yamaguchi, 1975b; Yamaguchi and Lucas, 1984). On coral reefs, benthic predation of larvae and newly settled recruits might be too high for benthic larval development or brooding behavior (Menge, 1975) to be a viable survival strategy. Two modes of reproduction are employed by some asteroids, one mode allowing the species to disperse, the other, the buildup of population numbers once colonization is established (Yamaguchi and Lucas, 1984).

7.2 Methods

Individuals of any species that exhibited signs of recent autotomy or fission were identified, collected, and measured. The presence of comets was considered indicative of asexual reproduction by means of autotomy, and recent disc fission, followed by regeneration of more than half the disc, indicative of reproductive binary fission. The frequency of occurrence of asexual products was recorded for each sampling period. Measurements were taken routinely of the number of arms and the length of the longest arm of each individual. Periodically, all arms of asexual specimens were measured, and details of obvious regeneration or autotomy were recorded.

In Linckia multifora and Echinaster luzonicus, the variation in mean individual size was recorded for each sampling period. In these two species, a one-way analysis of variance was calculated on the mean individual arm radius (R), within samples, both before and after a period of autotomy.

7.3 Results

Six species of asteroid at Heron Island are capable of asexual reproduction either by autotomy or binary fission. These species are Linckia guildingii, Linckia multifora, Echinaster luzonicus, Ophidiaster robillardi, Asterina anomala and Coscinasterias calamaria. The first four of these are capable of autotomy and can regrow a complete individual from nothing more than the distal half of an arm, with no need for any portion of the disc or madreporite to be included. The first stage of regeneration in the autotomized arm is called a comet after its characteristic shape. Comets were encountered frequently in these species and most of the individuals collected in this study had recently autotomized at least one arm, with the remaining arms being in various stages of regeneration. Individuals with all arms of equal length were very uncommon. On several occasions, recently autotomized arms were found alongside the parent animal in the field.

In large specimens of Echinaster luzonicus, the process of autotomy can proceed very quickly, and if the animals are handled roughly, arms can be autotomized immediately. If high water quality and a temperature comparable to that which occurs naturally, are not maintained when Linckia multifora and Echinaster luzonicus are kept in aquaria, freshly autotomized arms die, and the water becomes unsuitable for maintaining the adult animals.

In both Linckia multifora and Echinaster luzonicus the mean individual arm radius was observed to vary with periods of autotomy. The R/r ratio reflected periods of autotomy also. While specimens of Linckia guildingii and Ophidiaster robillardi that had undergone autotomy were observed throughout the study, only Linckia multifora and Echinaster luzonicus were common enough for this variation in mean size to be analyzed.

During the period of study, large changes in mean longest arm length were observed in both Linckia multifora and Echinaster luzonicus. At times of smaller mean individual size, the frequency of comet stages in the population was generally higher, but this varied between years. In 1978, the number of comet Echinaster luzonicus found in the field corresponded well with periods of lower mean individual size. For example, in May 1978, 29% of individuals were comets, whereas in August 1978, the proportion of comets was only 15%. This declined to about 5% in June 1979, and did not vary greatly over the remainder of the study. In Linckia multifora the proportion of comets in May, August and November 1978 was 32%. This declined to 8% in the

following two years. In 1981 and 1982, the proportion increased to 18%.

At Heron Reef, Asterina anomala and Coscinasterias calamaria reproduce by binary fission which results in two halves each regrowing to form two complete individuals. In this case a portion of disc containing a madreporite is always present as both species possess several madreporites on the disc. The remaining species while possessing great powers of regeneration are not capable of using autotomy or fission as a form of asexual reproduction. In all species that do not reproduce asexually, if parts of the body are autotomized, these parts die, and the remaining body regenerates the lost limbs.

7.4 Discussion

The size distribution of Linckia multifora and Echinaster luzonicus varied significantly over the study period (see Table 8). In both these species the autotomy rate varied within and between years, but the frequency of comet stages in the population was determined, in addition, by the survival rate of autotomized arms. This seemed to vary considerably from one year to another. Although comet stages of Linckia guildingii and Ophidiaster robillardi were found, there was no obvious temporal variation in their occurrence. Additionally, the abundance of these species was not sufficient to allow analysis of the change in mean individual size. Although individuals of Asterina anomala and Coscinasterias calamaria were found in varying stages of regeneration, once again, there appeared to be no temporal pattern in the occurrence of asexual stages (compare with Muenchow, 1978; Ottesen and Lucas, 1982).

At Heron Reef, the sexual reproductive effort appears to be very low in Echinaster luzonicus and Linckia guildingii. No sexual activity was recorded in Linckia multifora at all. Small individuals of these three species resulted invariably from autotomy. It would appear that asexual reproduction is the chief means of population maintenance in these three species. Ophidiaster robillardi is less common than either Linckia guildingii, Linckia multifora or Echinaster luzonicus at Heron Reef. On nearby Wistari Reef, the density of Ophidiaster robillardi in small patches on the reef crest was considerably higher than at Heron Reef. The spatial distributions of Linckia multifora, Ophidiaster robillardi and Echinaster luzonicus were highly clumped. This patchiness in abundance might be a result of local population increases following sexual colonization (Ottesen and Lucas, 1982). The only sexually reproducing species which showed very high spatial heterogeneity was Disasterina leptalacantha. The sticky eggs of this

species resulted in periodic high local recruitment. A low dispersion reproductive strategy is possessed by Linckia multifora, Disasterina leptalacantha and Echinaster luzonicus. These three asteroids occur at the highest local densities recorded during this study.

CHAPTER 8. CONSTANCY OF MEAN SIZE

8.1 Introduction

The fluctuations that occur in animal populations have been regarded as a measure of community stability (MacArthur, 1955; Frank, 1968; Den Boer, 1971; Jacobs, 1974; Goodman, 1975; Brown, 1981). Many authors believe that complex high diversity systems are characterised by relative constancy of species composition (e.g. Dunbar, 1960; 1972; Leigh, 1965; Margalef, 1963; 1974). They propose that populations of the component species do not vary to the extent demonstrated in more simple communities. Additionally, the interaction of competitors and predator / prey situations might prohibit the resource monopolisation so characteristic of dominant species in less diverse systems. Other authors (e.g. Connell, 1978; Sale, 1976, 1977; Sale and Douglas, 1984) believe that there is temporal variability in the community structure of the coral-reef organisms they have studied.

A paucity of juveniles characterises the population structures of large bodied, coral-reef starfish (Yamaguchi, 1973 a). It is possible that populations are maintained either by continual low recruitment or occasional high recruitment, each coupled with iteroparity. The juveniles are cryptic, and their apparent absence or rarity indicates that reproductive success is either constantly low, sporadic or both. Amongst coral-reef species, population outbreaks have been well documented for only Acanthaster planci. However, population changes in Linckia laevigata following Acanthaster outbreaks have been suggested by Laxton (1974) and Asterina burtoni is known to have extended its range into the Mediterranean Sea following its introduction through the Suez Canal (Achituv, 1969).

In most common species of coral-reef asteroid that have been studied, their reproductive strategy was directed towards the production of enormous quantities of gametes which were released directly into the surrounding water (Yamaguchi, 1973 a; 1977 a). If the mortality of the resulting larvae varied greatly from year to year, then we would expect years of noticeable recruitment followed by one or more years of little or no recruitment success. If the adult population is short-lived (e.g. two years), then the recruitment necessary to maintain the population must occur within this short period. If there were another consecutive year of recruitment failure, then the species would become locally extinct. In these short-lived species, juveniles should occur in sufficient numbers to be detected. If, however, the adults are long-lived, then the level of recruitment required to maintain the adult population could be extremely low per annum and we might expect to

see juveniles only occasionally.

If periods of high recruitment are required to maintain the population structure of a common species, the mean individual size of the populations should vary as a consequence of the influx of juveniles. In Ophidiaster granifer, when periods of recruitment occurred at Guam, the mean individual size of the population decreased (see Yamaguchi and Lucas, 1984). The mean individual size should increase progressively throughout the interval between periods of recruitment. In a large bodied species, such as Linckia laevigata, the mean individual size should increase slowly (dependent on growth rate), but might reach a size equilibrium determined by the availability of food (Paine, 1976). If periods of recruitment occurred, the mean individual size of the population should decrease. If recruitment did not occur, the mean individual size should increase slowly. The rate of increase in mean individual size will be determined by the average individual growth rate. This might be very slow in a species that is long lived.

8.2 Methods

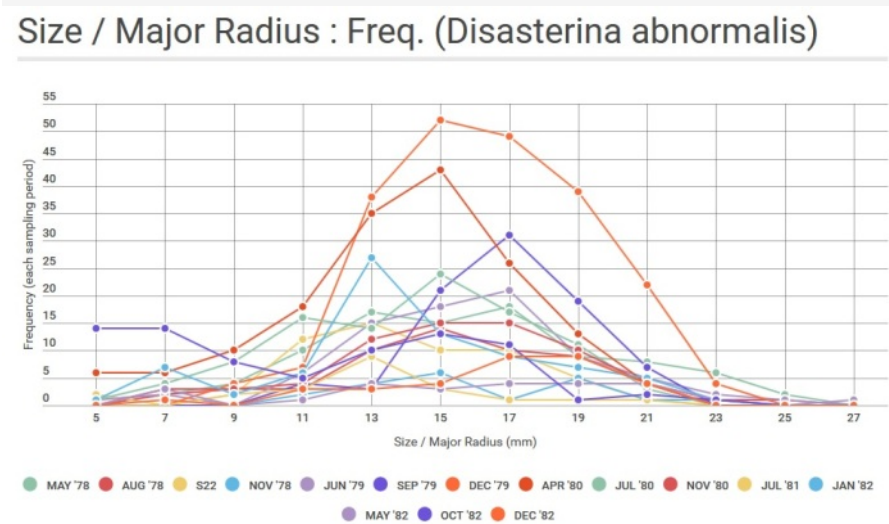
The size data for the more common species were analysed to see if there was any temporal variation in mean size for each species. A one-way ANOVA (ratio of variance in mean major radius (R mm) between and within sampling periods) for each species was calculated and the results are listed in Tables 5.1 – 5.10.

The mean size variation required to produce a probability level of .05 or .01 was very small for these relatively common species. Any probability not less than 0.001 represented only a small mean size variation compared with the size variation within each of the populations.

8.3 Results

Table 8.1 The significance of temporal size variation for each of the more common species. The grand mean (R mm), sample size (N), F statistic, degrees of freedom and probability level of the size variation over several sampling periods are tabled.

SPECIES	MEAN R	N	F	d.f.	P
Linckia guildingii	134	131	1.1	9,82	N/S
Linckia laevigata	127	516	1.7	11,459	<.05%
Linckia multifora	38	396	9.5	10,329	<.001%
Nardoa novaecaledoniae	88	361	3.2	11,295	<.01%
Nardoa pauciforis	104	233	2.2	11,179	<.05%
Disasterina abnormalis	15	1109	15.8	12,1054	<.001%
Echinaster luzonicus	48	988	11.4	10,883	<.001%



8.4 Discussion

From Tables 5.1 – 5.10, Figures 5.1a – 5.10a and Table 8.1, it can be seen that four of the large-bodied species, Linckia guildingii, Linckia laevigata, Nardoa pauciforis and Nardoa novaecaledoniae, did not vary their mean size greatly over the entire study period of five years. In two of these species, Linckia laevigata and Nardoa pauciforis, the mean size variation was significant at 0.05. In Nardoa novaecaledoniae, while significant at 0.01, this variation still represented only a small change in the mean size of the population over the entire study period.

Although four of the seven common species maintained a size distribution that did not vary greatly during the study period, the possibility that many of the species might demonstrate occasional

high recruitment success, when observed on a much larger time scale, cannot be rejected. If such recruitment occurred, it would manifest itself as oscillations in the mean individual size of that species. Asteroids are also known to possess highly plastic growth rates which can effectively disguise annual year classes.

It should be noted that a stable size distribution does not necessarily imply low recruitment and low mortality but can result from a balance of high recruitment and high mortality. Under conditions of high mortality and low recruitment, a population with a low growth rate can also manifest a stable size distribution but it would show a simultaneous decline in population density. This was not observed in the present study and the small change in the mean size of the large-bodied species suggests that Linckia guildingii, Linckia laevigata, Nardoa novaecaledoniae and Nardoa pauciforis are long-lived.

During this period, Linckia multifora, Disasterina abnormalis and Echinaster luzonicus showed mean size variations that were highly significant. This size variation was the result of periodicity in either sexual or asexual reproduction. In Linckia multifora and Echinaster luzonicus, the difference in size resulted from autotomy. High recruitment of juveniles was observed in only one small bodied, sexually reproducing species, Disasterina abnormalis. In the remaining species, the abundances were low, and statistically valid comparisons of what might have been temporal mean size variation could not be justified. This applied to Ophidiaster granifer that showed periodic recruitment when studied at Guam (Yamaguchi and Lucas, 1984), and Asterina burtoni which did not show significant mean size variation in the present study.

The relative stability of the size distributions of the common large-bodied species can be explained by assuming very slow growth of a predominant year class or a balance of recruitment and mortality within each of the species. It seems likely that a combination of both is involved. The paucity of juvenile asteroids, and the constancy of the size distributions in all the large bodied sexually reproducing species can be explained only by a life-history model which incorporates low adult mortality and includes the assumption of longevity.

The variation in mean size between populations of Linckia laevigata at different localities in the Indo-West Pacific could be caused by the presence of geographically asynchronous, dominant year classes. However, this is unlikely as this species did not alter its mean size greatly during the period of the present study. The highly plastic growth rate may be influenced by nutrition (see Wolda, 1970) or other

factors (e.g. disturbance) may cause both the higher density and smaller mean size. Dwarfism, resulting from high salinity, was described in Asterina burtoni by Price (1982).

The results of this study of coral-reef asteroids contrasts with data relating to laboratory rearing of Acanthaster planci which are claimed to demonstrate individual senescence at an age of approximately five years (Lucas, 1984). This finding, which appears to be inconsistent with the general biology of an often rare, large-bodied, and venomous animal, can be attributable to the laboratory rearing conditions (see Endean and Cameron, 1990 b). Additionally, a specimen of Acanthaster planci held in an aquarium at the Heron Island Research Station decreased to two-thirds of its original size within a period of 6 months. When adequate food is not available, regression in size might occur in many coral-reef asteroid species. At Heron Reef, the coral-reef asteroid community is not dominated by violently fluctuating size structures as might be expected from the work of Lucas (1984). All the large-bodied, sexually reproducing asteroids in this study existed with a stable size structure for the entire study period.

CHAPTER 9. RELATIVE ABUNDANCE AND DIVERSITY

9.1 Introduction

In addition to the high diversity of the coral reef ecosystem, a feature of this ecosystem is the large number of rare species within each taxonomic group. The general relation between the number of species and the number of individuals in a sample of a population was discussed by Fisher, Corbet and Williams (1943), who commented that species are not equally abundant, even under conditions of considerable uniformity. They went on to state that the majority of species are comparatively rare while only a few are common.

It is not known whether the rarity of a species is indicative of its low competitive ability or alternately whether the species is restricted to specialised microhabitats with excess recruitment eliminated by predators (Hairston, 1959; Kunin and Gaston, 1993). The relative abundances of the species in a diverse assemblage are often distributed over many orders of magnitude. As a result, qualitative representations of abundance such as common, moderately abundant or rare must be arbitrary in their assignment.

Many different mathematical models have been proposed to describe satisfactorily the relationship that exists between the relative abundances of different species in an assemblage. While each model has been criticised extensively (Hurlbert, 1971; Abbott, 1983; Connor and McCoy, 1979; Connor, McCoy and Cosby, 1983; Martin, 1981; McGuiness, 1984; Pielou, 1981; Sughihara, 1981), each attempt to quantify the degree of variation in the relative abundances of the different species. The most noticeable result of this abundance variation is the different rates at which species accumulate with increased sampling in different assemblages.

9.2 Methods

The population density of each species and the relation between sample area and the number of individuals in the sample was calculated in Chapter 4. The relation between sample area and the total number of species in the sample (the species:area curve) was also calculated from the traverse data. The cumulative number of species was compared with the cumulative area of the traverses (starting at the completion of Traverse 1 and continuing through to the completion of Traverse 72). This comparison was also undertaken with the natural logarithm of the cumulative area of the traverses.

Shannon's Evenness Index (see Pielou, 1981) which is the expression (S P(log P)) / log S, where P is the proportion of each species in the community, and S is the total number of different species, is often used to display the relative richness of various communities. Shannon's Evenness was calculated for each traverse individually and cumulatively starting with Traverse 1 and ending with Traverse 72.

The relation between the numerical abundance of each species and the rank abundance of each species was calculated by ordering the numerical abundance from most common (rank 1) to least common (equal rank 20 for five species). Percent relative abundance was the ratio of the numerical abundance of each species to the total asteroid abundance.

9.3 Results

Table 9.1 lists the numerical, relative and rank abundances of each species located on the intertidal traverses. Figure 9.1a graphs the relation between the numerical abundance of a species and its rank abundance. Figure 9.1b graphs the relation between (log) relative abundance and rank abundance. Figures 9.2a,b graph the species : area and species : (log) area relation. Figures 9.3a,b graph the relation between Shannon's Evenness and cumulative area and cumulative (log) area. Natural logarithms were used in all these calculations. Shannon's Evenness as a measure of diversity has the advantage that the index is a ratio of attained diversity over maximum possible diversity and is therefore independent of the base of logarithm which has been chosen.

Table 9.1

The numerical abundance, relative abundance, and abundance rank of inter-tidal asteroids at Heron Reef.

SPECIES	NUMERICAL	RELATIVE	RANK
Culcita novaeguineae	15	**	13
Asteropsis carinifera	3	*	19
Dactylosaster cylindricus	1	*	20
Fromia elegans	16	**	12
Fromia milleporella	1	*	20
Gomophia egyptiaca	6	*	16
Linckia guildingii	116	***	8
Linckia laevigata	509	***	3
Linckia multifora	522	***	2
Nardoa novaecaledoniae	326	***	5
Nardoa pauciforis	187	***	7
Nardoa rosea	1	*	20
Ophidiaster armatus	4	*	17
Ophidiaster confertus	4	*	17
Ophidiaster granifer	116	***	9
Ophidiaster lioderma	1	*	20
Ophidiaster robillardi	24	**	10
Asterina anomala	17	**	11
Asterina burtoni	208	***	6
Disasterina abnormalis	500	***	4
Disasterina leptalacantha	7	*	14
Tegulaster emburyi	1	*	20
Echinaster luzonicus	1402	****	1
Coscinasterias calamaria	7	*	14

* Very rare <10 :** rare 11-100 :*** common 101-1000 :**** abundant>1000

9.4 Discussion

The generally low abundances of most of the species of starfish at Heron Reef precluded the use of quadrats in general sampling. Because the traverse method will miss many cryptic individuals and provide only an approximate area measurement, the species diversity and species accumulation figures are only approximate. It would appear from Table 4.1 that most species occurred at a density that was less than one individual per hectare, with many species being far less abundant. It should be noted that traverse sampling will underestimate the density of all cryptic species and will also fail to detect species that are both rare and cryptic.

McGuiness (1984) suggested that the use of species : (log) area or (log) species : (log) area for the display of the species : area relationship should be based on the underlying relative abundances of the species. The slope of the species : (log) area relationship, the slope of the (log) relative abundance : rank abundance relationship and Shannon's Evenness index are all indices of diversity. These allow a direct comparison to be made between different assemblages. Not only do

these indices consider the number of species, but they also express the inherent range of abundance between most common and least common within the assemblage (Connor and McCoy, 1979; Connor and Simberloff, 1979; Connor et al., 1983).

Figures 9.1a,b show that the four most common species account for 70% of the total number of individuals in this assemblage. However, even Echinaster luzonicus, the most abundant species, had an average density of only 16 specimens per hectare. Of the 24 species of asteroid that occurred in the traverse samples, five species occurred only once. Presumably the species which were not found during this study, but which are known from the locality, occur with even less frequency than these five. Less than ten specimens of each of another six species were located on the intertidal traverses. Hence, 11 of the 24 species are regarded as very rare. Less than 25 specimens of another three species were found and these are regarded as rare. Thus, a majority of the asteroid species found at Heron Reef are rare or very rare.

The slope of the regression line in Figure 9.1b is a measure of the diversity of this asteroid assemblage. The steeper the line the greater the range of relative abundance within a certain group of species. The less equal the relative abundances, the lower the diversity as measured by most diversity indices. Community studies often show a log-normal relationship in relative abundance, in which most species occur with close to the average abundance (Pielou, 1981). This assemblage of coral-reef asteroids does not clearly demonstrate this relationship, but this result may be attributable to an inadequate number of both species and individuals in the present study. The order of the species in Figures 9.1a,b is that of numerical abundance. If biomass or some other parameter was chosen as a measure of abundance, then the order of the species may change but the slope of the regression line might not alter greatly.

Figures 9.2a,b illustrate the species : area curve for the Heron Reef asteroid assemblage. The slope of the (log) area regression line is independent of the units used to measure area. Whether they be square metres or hectares, providing the habitat continues, the species will accumulate at a rate determined only by the relative abundances of the species in the assemblage. If there is some finite species pool which obviously cannot be exceeded, then the curve will become asymptotic.

The pronounced dips in Figures 9.3a,b are a result of small scale patchiness in the distribution of Echinaster luzonicus and Disasterina abnormalis. After continued sampling, the effect of this high localised

abundance was rendered insignificant in the total diversity.

Figures 9.1a to 9.3b all relate to the one ecological parameter, namely the relative abundances of the species within this assemblage. This will determine the rate at which the species accumulate in a species : area curve, as well as the diversity as measured by most diversity indices.

The richness of the coral-reef asteroid assemblage at Heron Reef is unable to be compared directly with that of other coral-reef asteroid assemblages either on the Great Barrier Reef or elsewhere. This is because the extent of sampling has not been quantified in the majority of biogeographical studies. Because the area sampled determines the number of species in a sample of any assemblage (Fisher, Corbet and Williams (1943), the large number of species found at Heron Reef may be a result of the intensive sampling. Even so, it would appear from the linearity of Figures 9.2b that additional species of starfish occur intertidally at Heron Reef, but these species are either extremely rare or cryptic.

It is apparent that Heron Reef carries a rich and diverse asteroid fauna, 24 species belonging to six families having been found intertidally in 120 hectares during this study. The linearity of the species : (log) area relationship for the intertidal asteroid assemblage at Heron Reef indicates that additional species are still to be found. Indeed, Mithrodia clavigera was located subsequent to the traverses and Endean (1956) found three species (Acanthaster planci, Ophidiaster watsoni and Anseropoda rosacea) in the area of the traverses that were not found during the current study.

CHAPTER 10. GENERAL DISCUSSION

Population density, size-frequency, and reproductive data on an assemblage of shallow water, coral-reef starfish (Asteroidea) were gathered over five years at Heron Reef. Heron Reef, which is located near the southern end of the Great Barrier Reef, has not been known to carry an outbreak of the crown-of-thorns starfish (Acanthaster planci) and its coral cover is well developed. While there has been detailed study of the starfish assemblages on some reefs that have recently undergone Acanthaster planci population outbreaks (Yamaguchi, 1975 b; 1977 a), the composition of these assemblages may well be different from pre-outbreak assemblages.

Abundance, size-frequency, and reproductive data were collected by means of intertidal traverses which ran between the cay and the reef crest (0.5 to 2 kilometers apart) and also between two points both on the reef crest (0.5 to 6 kilometers apart). Most traverses included both reef flat and reef crest zones, and all exposed starfish within a 4-meter width were collected. A selection of large and small, dead coral slabs occurring on these traverses were overturned and cryptic specimens located beneath these slabs were collected also. In total, 72 intertidal traverses were conducted covering an area of approximately 120 hectares (1.2 square kilometers). Cryptic species were also sampled using meter square quadrats in particular areas where previous traverse sampling had shown that starfish abundance was relatively high. Subtidal specimens of starfish were collected on the reef slope and off-reef floor using SCUBA.

Of the 25 starfish species found on Heron Reef, Asteropsis carinifera, Dactylosaster cylindricus, Fromia milleporella, Linckia laevigata, Nardoa novaecaledoniae, N. pauciforis, Ophidiaster confertus, O. granifer, O. lioderma, O. robillardi, Asterina anomala, A. burtoni,

Disasterina abnormalis, D. leptalacantha, Tegulaster emburyi, Mithrodia clavigera and Coscinasterias calamaria were located only in intertidal regions. Linckia guildingii, L. multifora and Echinaster luzonicus were found predominantly in intertidal regions but some specimens were located sub tidally. Culcita novaeguineae, Acanthaster planci, Fromia elegans, Gomophia egyptiaca and Neoferdina cumingi were located predominantly in subtidal habitats but are known to occur intertidally. Culcita novaeguineae seemed to mainly inhabit the deeper coral pools adjacent to the lagoon. The low occurrence of Culcita novaeguineae on the intertidal traverses is because the traverses avoided this slightly deeper-water habitat. While Culcita novaeguineae, Fromia elegans, Gomophia egyptiaca, Linckia multifora and Echinaster luzonicus were sometimes found at the base of the reef slope, they were never observed on the sea floor away from the reef. There are no published records of these species from the off-reef floor zone (see Clark and Rowe, 1971).

"Reef" echinoderm species were separated from "mainland" species based on their habitat requirements by Endean (1956) who discussed the biogeographical relationships of Great Barrier Reef species. Except for Ophidiaster confertus and Coscinasterias calamaria, which are essentially temperate species, 23 asteroid species found at Heron Reef can be regarded as coral-reef species and their distribution differs from species such as Astropecten polyacanthus, Iconaster longimanus, Pentaceraster regulus, Leiaster leachi, Nardoa rosea, Ophidiaster armatus, Tamaria megaloplax and Echinaster stereosomus. These latter species appear to be predominantly off-reef, sea-floor species that are widely distributed throughout the shallow waters of tropical and sub-tropical Queensland. The predominantly reefal distribution of the long-spined, corallivorous species, Acanthaster planci, contrasts with that of its generally deeper water, short-spined, molluscivorous relative, A. brevispinus. Only small fissiparous specimens of

Coscinasterias calamaria were located on Heron Reef. Large adults of this and other forcipulatid species are predators in temperate communities. Both Ophidiaster confertus and Coscinasterias calamaria appear to be predominantly temperate species that occur in Australian mainland waters, but which have extended their ranges to reefs at the southern end of the Great Barrier Reef.

The finding of Iconaster longimanus, Asteropsis carinifera, Dactylosaster cylindricus, Fromia elegans, Linckia multifora, Ophidiaster armatus, Ophidiaster lioderma, Ophidiaster robillardi, Tamaria megaloplax, Asterina anomala, Disasterina abnormalis, Tegulaster emburyi, Mithrodia clavigera, Echinaster stereosomus and Coscinasterias calamaria represent new records for Heron Reef. In some cases, these represent new records for the Great Barrier Reef, and in other cases known ranges on the Great Barrier Reef have been considerably extended. This study has also provided the first record of the predominantly temperate species, Coscinasterias calamaria on the Great Barrier Reef.

The distinguishing characteristic of coral-reef species of starfish is their possession of a spatial distribution that never extends into the deeper parts of the off-reef floor zone. Such a spatial distribution would preclude between-reef migration by post-larval stages of these species. It is not known why some species of starfish are essentially restricted to coral reefs, but it is likely that such species would differ in their physiological and / or ecological requirements from species that occur elsewhere. While the intertidal region of a coral reef undergoes both temperature and salinity fluctuations (Maxwell, 1968), a substrate of coral sand and rubble (aragonite not calcite) would ensure complete carbonate saturation of the waters and hence the waters would be well buffered against pH changes. Some species of starfish that occur exclusively in association with coral reefs may have narrow

pH tolerances. Other species may have evolved interdependencies that involve settlement or survival conditions that are only present within the coral reef ecosystem. Likewise, with respect to the coral reef ecosystem itself, it might be expected that species that occur predominantly in one of the major zones of a coral reef (e.g., the reef flat) would differ in their physiological and / or ecological requirements from species that occur in several of these zones. For example, they might differ in their degree of tolerance to sub-aerial exposure at low tide or in their biotic associations.

Patches of localized high density were observed within the populations of some of the smaller-bodied species of coral-reef starfish that were studied. However, each of these patches appeared to be restricted to a very small area. For example, the small-bodied starfish Disasterina abnormalis occurred at an average density of over eight individuals per square meter at one location on the northern reef crest but 100 meters away (still on the reef crest) its density was less than one individual per square meter. This region of high density of Disasterina abnormalis appeared to be confined to a narrow strip behind a rubble bank and this species was not found on 25 of the 72 traverses that were made. In this region, Disasterina abnormalis was highly clumped (at the meter square scale) in one sampling period and randomly distributed in another sampling period.

Echinaster luzonicus was the most abundant starfish found on the intertidal traverses and Linckia multifora was the next in order of decreasing abundance. Both small-bodied species were found in relatively high numbers in some regions of the reef crest. The large-bodied starfish Linckia laevigata was third in order of decreasing abundance on the traverses but its maximum density did not approach that of either of the preceding species anywhere at Heron Reef. The density of Linckia laevigata at Heron Reef appeared to be low

compared with its density on reefs that are known to have carried an outbreak of Acanthaster planci (Laxton, 1974; Yamaguchi, 1977 a; Thompson and Thompson, 1982; Klumpp and Pulfrich, 1989). Laxton (1974) suggested that Linckia laevigata may either increase its numbers or extend its range following outbreaks of Acanthaster planci. Disasterina abnormalis was fourth in order of decreasing abundance and occurred at the highest local density of any species of starfish during this study.

The intertidal traverses made during this study covered an area of 125 hectares. Over 1400 individuals of Echinaster luzonicus were located and over 100 individuals of each of another 8 species were located. However, fewer than 25 individuals of each of the remaining 15 species were located. The low starfish density found at most locations on Heron Reef contrasts markedly with the high densities recorded for asteroids of temperate communities (Loosanoff, 1961; 1964; Mauzey et al, 1968; Menge, 1975; Dayton et al, 1977; Birkeland et al, 1982; Stevenson, 1992).

Traverse sampling resulted in the location of a total of 24 species of intertidal starfish. For 10 of these species, enough individuals were obtained for reproductive analysis and for 7 of these species size-frequency variation was examined over different sampling periods. Traverse sampling enabled data to be gathered on a large spatial scale (125 hectares) which facilitated both the collection of sufficient specimens for reproductive and size-frequency analysis as well as the determination of large-scale non-randomness in the spatial distribution of these species.

While the intertidal traverse data did not allow small-scale analysis of either spatial or temporal abundance variation, the starfish assemblage at Heron Reef clearly embraces a highly diverse and

spatially heterogeneous group of species. Individuals of each species were extremely non-random (clumped) in their spatial distribution. Only Echinaster luzonicus was sufficiently abundant and widespread to be found on all but three of the traverses. Linckia laevigata and Nardoa novaecaledoniae were not located on 10, Nardoa pauciforis was not located on 19, Linckia multifora was not located on 22, Disasterina abnormalis was not located on 25, Asterina burtoni was not located on 26 and Linckia guildingii was not located on 34 of the 72 traverses made. Representatives of the remaining species were not found on most of these intertidal traverses.

Except for Echinaster luzonicus, the abundance distributions of all of the species had a modal traverse density of zero individuals per hectare. This indicated that, except for Echinaster luzonicus, each coral-reef starfish species was not represented on a large number of the traverses. The more common of these species possessed a bimodal abundance distribution which indicated that they were non-random (patchy) in their spatial distribution. For these species, there were many traverses where both zero and a relatively large number of individuals per hectare were recorded and very few traverses where intermediate (mean) densities occurred.

Table 4.1 lists the mean density per hectare and the variation that occurred in the mean density of each species between traverses. In all species the standard deviation was greater than the mean density. These data together with the bimodal population distribution data (Figures 4.2 to 4.12) indicate that large scale aggregation occurs in all the species with the possible exception of Echinaster luzonicus. A stratified-random sampling procedure, using multiple belt transects would have allowed a detailed comparison of starfish abundances between different habitats. However, when used on a reef that has low general starfish abundance, such a sampling method would not have

located enough individuals in the limited time available for field studies at Heron Reef to permit a statistically valid size-frequency and reproductive analysis.

A mode in the abundance distribution was recorded at between three and 10 individuals / hectare in six species (rank 1 – 6) and at between one and three individuals / hectare in another six species (rank 7 – 12). The remaining twelve species (rank 13 – 20) were encountered so infrequently that the only mode in the abundance distribution of each species was at zero individuals per hectare. Five species were sufficiently uncommon (rank 20) to be encountered on only one intertidal traverse during the entire study.

Culcita novaeguineae, Fromia elegans, Gomophia egyptiaca and Nardoa rosea were encountered much more frequently in sub-tidal traverses than they were on intertidal traverses. Disasterina leptalacantha was recorded more frequently at Heron Island by Endean (1957) than it was in this study, but there may have been confusion between the two similar congeneric species in the earlier study. Similarly, the ecological distinction between Asterina anomala and Asterina burtoni is unclear. The observed variation in the abundance of Asterina burtoni at Heron Reef is consistent with the results of Achituv and Sher (1991), but the mode of reproduction appears to be different.

The very small and highly cryptic species Disasterina abnormalis occurred periodically with high abundance at one location on the inner reef crest. It was possible to sample this species in this localized habitat by means of meter square quadrat sampling (Table 4.2). The data obtained do not represent the abundance of this species generally but serve to illustrate clearly the enormous spatial and temporal variation that occurs in the population distributions of this

opportunistic species.

Although the diets of the coral-reef starfish species encountered were not studied in detail, many of them appeared to feed on epibenthic felt. In every coral reef zone, some species sought no refuge and occurred in exposed situations. Clear examples of niche (dietary or microhabitat) specialization are known only for Culcita novaeguineae and the predominantly subtidal species Acanthaster planci both of which feed primarily on corals. Competitive interactions were not studied, but many species occurred at a sufficiently low density that they may not be resource limited.

Because of the patchy nature of the spatial distributions of all the coral-reef asteroid species, size-frequency analysis over multiple sampling periods (Tables 5.1 to 5.12 and Figures 5.1a to 5.10d) was considered the most appropriate means of establishing the existence of population stability. Obvious changes in abundance due to either sexual or asexual recruitment, and significant changes in mean individual size were observed in the populations of Linckia multifora, Disasterina abnormalis and Echinaster luzonicus (Table 8.1 and Figures 8.1a to 8.3c). While some recruitment and some change in abundance was noticed in both Ophidiaster granifer (parthenogenetic) and Asterina burtoni (hermaphroditic), no significant change occurred in the mean individual size of either species. Linckia guildingii, Linckia laevigata, Nardoa novaecaledoniae and Nardoa pauciforis exhibited only small changes in mean individual size and these species did not fluctuate greatly in abundance during the period of study. Also, the population structure of these species appeared to be adult dominated, and juveniles were encountered only rarely.

The remaining species were not found in sufficient numbers for meaningful statistical analysis of size-frequency data. Their

populations were sparse, and juveniles were not encountered except for one specimen each of Culcita novaeguineae, Fromia elegans and Gomophia egyptiaca. Their populations appeared to be adult dominated. Juveniles of Culcita novaeguineae and Fromia elegans were not encountered sub tidally despite the existence of a subtidal population of adults. One juvenile of Acanthaster planci was located at the base of the reef slope.

Culcita novaeguineae and many other coral-reef starfish species were not encountered in sufficient numbers to warrant an examination of their population stability. The study of Laxton (1974) appeared to show a greater abundance of Linckia laevigata on the reef flat at Heron Reef than was observed in this study. Laxton suggested that this species may vary its distribution range following outbreaks of Acanthaster planci. It is possible that large-bodied species of starfish, such as Linckia laevigata, undergo large scale aggregation behavior but the limited duration of this study precluded examination of such long period fluctuations.

Grassle (1973), Sale and Dybdahl (1975), Talbot et al. (1978) and Hutchings (1981) all found that most coral-reef species are rare. Endean and Cameron (1990 a) mention that the high incidence of rare species in the coral-reef community contributes markedly to species diversity. Some of the rarer species of coral-reef starfish are known from only a few specimens and their low-density populations defy our normal understanding of population dynamics and reproductive strategies. It is not clear how these species survive or whether their populations are predator, resource or recruitment limited. Species such as Tosia queenslandensis, Ophidiaster lioderma and Tegulaster emburyi have always been considered rare throughout their geographical range. Although nothing is known of their reproductive cycles, if they are truly rare and valid “biological” species, then they

might be expected to exhibit mechanisms such as population aggregation, asexual reproduction, parthenogenesis, or hermaphroditism that would facilitate their persistence at low population densities.

Inter-coelomic injection with the hormone 1-methyl adenine was used to determine the sex ratio, reproductive maturity, and type of larval development of several of the species. It can be seen from Tables 6.1 to 6.8 and Figures 6.1 to 6.8 that eight of the more common species appeared to demonstrate an annual sexual reproductive cycle. Disasterina abnormalis possessed small (non-yolky) sticky eggs that adhered to the substrate immediately following their release from the gonopores. Small juveniles of Disasterina abnormalis were relatively common in one highly localized area at Heron Reef, but high settlement was not observed in any of the other species. The remaining seven species possessed eggs that dispersed and underwent either planktotrophic or lecithotrophic larval development. No species were observed to brood larvae.

Culcita novaeguineae, Acanthaster planci, Linckia guildingii and Linckia laevigata were observed releasing eggs that contained little yolk and underwent planktotrophic development. Fromia elegans, Gomophia egyptiaca, Nardoa novaecaledoniae, Nardoa pauciforis, Ophidiaster granifer and Echinaster luzonicus were observed releasing eggs that contained large amounts of yolk and underwent lecithotrophic development. Specimens of both Linckia multifora and Asterina burtoni were injected regularly but did not release gametes during the entire study.

Vance (1973) and Yamaguchi (1973 a, 1973 b, 1977 b) suggested that lecithotrophic development is an adaptation to high predation or starvation of larva because with this development the length of larval

life can be shorter than with planktotrophic development. On Heron Reef, and possibly the Great Barrier Reef in general, where many reefs exist in relatively close proximity, lecithotrophic genera such as Nardoa, Fromia and Echinaster might be expected to be better represented than they are on widely scattered atolls. At Heron Reef, the larger-bodied species namely, Culcita novaeguineae, Acanthaster planci, Linckia guildingii and Linckia laevigata all liberated dispersing, small eggs that underwent planktotrophic development while the smaller-bodied species, together with Nardoa novaecaledoniae and Nardoa pauciforis (both intermediate in body size), all liberated larger eggs that underwent lecithotrophic development. The small, sticky eggs of Disasterina abnormalis resulted in high localized settlement and this strategy appeared to be unique amongst the starfish species that were studied at Heron Reef.

In addition to the species that demonstrated a sexual reproductive cycle, Linckia guildingii, Linckia multifora, Ophidiaster robillardi and Echinaster luzonicus reproduced asexually and exhibited comet stages while Asterina anomala and Coscinasterias calamaria reproduced asexually by binary fission. All small specimens of these species exhibited the characteristics of either autotomous propagation (see Rideout, 1978) or binary fission. While all of the arms might look quite similar in some small individuals of autotomous species, the original arm from which the others regenerated was always apparent following closer examination. All specimens of fissiparous species showed signs of recent binary fission.

While specimens of both Linckia guildingii and Echinaster luzonicus were observed releasing gametes in response to injection with 1-methyl adenine, no sexually propagated juveniles were observed in the populations of any species that reproduced asexually. Except for Linckia guildingii, large bodied species of coral-reef starfish do not

appear to have a small scale (low dispersion) reproductive strategy. This could indicate that survival of offspring is more likely away from adult populations. The advantages of a high dispersion reproductive strategy must be balanced against the high dispersive loss resulting from the relative isolation of reefs of the Great Barrier Reef and elsewhere.

Linckia multifora and Echinaster luzonicus were the only asexually reproducing species in which high rates of autotomy were observed and the location of comet stages and adults in various stages of regeneration is evidence of relatively high asexual recruitment. These three species had the highest localized abundances of any of the coral-reef starfish but also had highly patchy spatial distributions. The remaining species never occurred at densities comparable with these species even though the average density of Linckia laevigata was higher than the average density of Disasterina abnormalis. While comet stages and adults in various stages of regeneration were observed in Linckia guildingii, this species did not show evidence of high asexual recruitment.

With the exception of Disasterina abnormalis (see Chapter 6), all the species of starfish at Heron Reef either possessed a planktonic dispersive larval phase or were not observed to reproduce sexually. The largest-bodied persistent species released planktotrophic eggs while the opportunist species were either lecithotrophic, hermaphroditic (Asterina burtoni), parthenogenetic (Ophidiaster granifer) or solely asexually reproducing (Linckia multifora). Nardoa novaecaledoniae, Nardoa pauciforis and Gomophia egyptiaca would appear to be of intermediate position and the taxonomic position of Asterina anomala is unclear.

All the large-bodied species studied liberated either eggs or sperm

directly into the water column and fertilization was external. While possible pairing was observed in crowded aquaria (following injection with 1-methyl adenine), no species were observed mating in the field as has been recorded by Run, Chen, Chang and Chia (1988) for the tropical species Archaster typicus. Slattery and Bosch (1993) also recorded mating behavior in an Antarctic species of starfish.

Ormond et al. (1973) discussed the consequences of spawning aggregations of Acanthaster and suggested that the increased proximity of adult starfish may enhance the chances of fertilization, especially if synchronous spawning takes place. It was suggested by Lucas (1984) that a conspecific stimulus would induce synchronous spawning in Acanthaster planci and a delayed spawning activity in dispersed individuals of Acanthaster planci was observed by Okaji (1991). It was suggested that this delay reflected less frequent stimulus from conspecifics in dispersed populations compared with aggregated populations and that synchronous spawning induced by such stimulus would lead to higher rates of fertilization when the animals formed an aggregation. Evidence of the existence of sexual pheromones in starfish was presented by Miller (1989).

The effect of sperm dilution, adult aggregation, and synchronous spawning upon the fertilization of sea-urchin eggs was reported by Pennington (1985). Pennington concluded that significant fertilization occurred only when spawning individuals are closer than a few meters. The consequences of water mixing and sperm dilution for species that undergo external fertilization were discussed by Denny and Shibata (1989) who found that only a small fraction of ova was fertilized other than in densely packed arrays. They commented that the low effectiveness of external fertilization may change the way one views the planktonic portion of such life cycles and suggested that this could serve as a potent selective factor. For the rarer sexually reproducing

species, it is apparent that aggregation resulting in the occurrence of an opposite sexed conspecific within the effective fertilization distance is a condition precedent to successful reproduction. The degree of reproductive success may be strongly dependent on just how close the rare spawning individuals are to each other. While the results of Babcock and Mundy (1992) appear inconsistent with these previous studies, the population density and degree of adult aggregation would be highly relevant factors for both the synchrony of spawning and the level of egg fertilization in externally fertilizing dioecious species. If a low-density starfish population is highly dispersed, then the degree of egg fertilization would be much lower than if aggregation occurred.

The above factors influence recruitment as do many other factors such as dispersion loss (Atkinson et al, 1982; Dight et al., 1990 a, b; Black and Moran, 1991; Wolanski, 1993) and starvation of larvae (Birkeland, 1982; Olsen, 1987). These factors, together with the mortality of juveniles prior to first reproduction (Endean, 1977; 1982; McCallum et al, 1989), might result in this assemblage being recruitment limited as suggested for certain species of coral-reef fish by Doherty (1982). If the process of recruitment is completed when an organism enters the breeding population, then a species could be regarded as recruitment limited if mortality of its larvae or juveniles was sufficiently great to maintain adult populations at a low density. This may occur as a result of either low egg fertilization or high mortality of larvae or juveniles.

On reefs such as Heron Reef that have low adult starfish abundance, predation of adult starfish appears to be a rare event and was not studied because of logistic constraints. While the giant triton (Charonia tritonis) is a voracious predator of large juvenile and adult starfish (Endean, 1969; Pearson and Endean, 1969), no specimens of this species were observed at Heron Reef either sub tidally or on intertidal traverses during the entire study. The giant triton is cryptic

and it is extremely difficult to survey the population density of this predator. It is likely that there are other predators of coral-reef starfish, particularly fishes. Other predators (see Endean and Cameron, 1990 b) have been found for Acanthaster planci. If starfish populations are stable then mortality (including lethal predation) will match recruitment which appeared to be extremely low in the populations of large bodied coral-reef starfish. If starfish populations are maintained at a low adult density, then predation on pre-adults could be a major factor in controlling the assemblage.

An increase in anti-predatory structures with decreasing latitude was found by Vermeij (1978) and Blake (1983) suggested the existence of a similar pattern in sea stars. Pearson and Endean (1969) and McCallum et al. (1989) reported a high incidence of sub-lethal predation in populations of Acanthaster planci. Blake (1983) commented that the asteroid fauna of the Indo-West Pacific are dominated by the order Valvatida and members of this order have the best developed anti-predatory devices. Yamaguchi (1975 b) commented on the difference between adult and juvenile asteroid habits and suggested that the heavy armor of exposed adult asteroids might reflect heavy predation pressure.

In addition to the protection afforded by structural features, many species of starfish are protected from generalist predation by the possession of skin toxins (Riccio et al., 1982, 1985; Gorshkov et al., 1982; Minale et al., 1984; Narita et al., 1984; Noguchi et al., 1985 a,b; Miyazawa et al., 1985; 1987; Kicha et al., 1985; Shiomi et al., 1988; Shiomi et al., 1990; Zagalsky et al., 1989; Iorizzi et al., 1991; Bruno et al., 1993; Casapullo et al., 1993). These skin toxins have been shown to be toxic to some fish species (Rideout, 1975). The role of echinoderm toxins as a defense against predation has been discussed extensively (Bakus, 1974; Green, 1977). Cameron and Endean (1982)

discussed the role of venomous devices and toxins as defenses against predation and Endean and Cameron (1990 a) have noted that persisters are often toxic. There is little information available on the toxicity of juvenile starfish to potential predators. Eggs and juveniles of Acanthaster planci are known to carry toxins. It has been proposed that the production of toxins for defense incurs an energy cost which is balanced against the probability of mortality (Eckardt, 1974) but in some species, toxins might be metabolic by-products that incur no energy cost in their synthesis.

In some groups of starfish behavioral mechanisms are used as defenses against predation and Blake (1983) suggested that both Luidia and Astropecten have broad open ambulacral furrows because they were predators on active solitary forms where increased skeletal mobility was essential. Because both these active, hunting genera live on and within unconsolidated sediment they avoid predation by burrowing which is facilitated by the paxillose nature of their aboral surface.

Another behavioral defense possessed by asteroids is the autotomy of arms. Of the coral-reef starfish studied, Linckia guildingii, Linckia multifora, Ophidiaster robillardi and Echinaster luzonicus are capable of regenerating a complete individual from the distal section of one arm. These autotomous species were extremely aggregated in their spatial distribution, suggesting that population growth occurs with little dispersal of individuals.

In species of starfish that do not reproduce by autotomy, specimens are often observed in various stages of regeneration following loss of one or more arms. McCallum et al (1989) reported that 40% of the adult individuals in a population of Acanthaster planci showed signs of arm regeneration. Cameron and Endean (1982) suggested that autotomy is an adaptation to predation and Birkeland et al (1982)

observed autotomy in their study of asteroid predatory interactions. At Heron Reef, many individuals were observed in various stages of regeneration following autotomy of one or more limbs. A number of tropical asteroids are known to undergo regular autotomy (Rideout, 1978; Yamaguchi, 1975 b) and Blake (1983) commented that interpretation of the skeleton can be difficult as it has more than one function and protection against predation can be accomplished by many mechanisms (e.g. Bullock, 1953; Feder, 1963; Mauzey et al., 1968; Ansell, 1969; Birkeland, 1974; Phillips, 1976; Dayton et al., 1977; Jost, 1979; Schmitt, 1982; Stevenson, 1992; Iwasaki, 1993).

In the species that reproduce by autotomy, it is not known to what extent the autotomization of a limb is caused by physical disturbance such as predation. While direct predation was not observed, large individuals of the large-bodied species of starfish often had their arms intertwined with the substrate such that they were difficult to dislodge. In the large-bodied species that only reproduce sexually, parts of a limb and even one or two whole limbs were observed to be missing from some individuals. The existence of such behavior together with the observations of missing arms in species that do not reproduce asexually, indicates that sub-lethal predation does occur. Whether it is significant in the regulation of the Heron Reef asteroid assemblage will depend on the age structures of the populations. Sub-lethal predation of adults will be especially important if a species is long lived.

This study has examined the population dynamics of both relatively common and relatively rare species of coral-reef starfish. Although some species were not sufficiently numerous to provide statistically satisfactory numbers of records, data were gathered on their habitat, size, spatial pattern and relative abundance. It is clear that the majority of species of intertidal starfish at Heron Reef were sufficiently

uncommon to preclude small scale methods of population examination. There is considerable disagreement over the accuracy of large scale methods (manta tow) to examine subtidal populations of starfish (Fernandes, 1990; Fernandes et al., 1990; Moran and De'ath, 1992 a, b). However, the determination of large scale, non-random variation in the distribution of any species is a condition precedent to the determination of its overall abundance. In the estimation of average density, methods of both sampling and analysis must adequately consider the high standard error of the mean. All conclusions must have due regard to the bimodality and skewness of the abundance distributions of starfish.

Some species, namely Disasterina abnormalis, Asterina burtoni, Ophidiaster granifer, Linckia multifora and Echinaster luzonicus, could be regarded as opportunist species as they were characterized by possessing relatively abundant populations with relatively large fluctuations in mean individual size. These invariably small-bodied species demonstrated all of the typical opportunist characteristics which are short life, high recruitment and high mortality (see Endean and Cameron, 1990 a).

Other species, namely Culcita novaeguineae, Linckia laevigata, Linckia guildingii, Nardoa novaecaledoniae and Nardoa pauciforis could be regarded as persistent species and were characterized by less abundant populations with relatively smaller fluctuations in mean individual size. These invariably medium to large bodied species demonstrated all of the typical persister characteristics which are long life, low recruitment and low mortality. A large proportion of coral-reef starfish were sufficiently uncommon to preclude any analysis of either their abundance or size distributions. Apart from the knowledge that they remained rare through the study period of 5 years, little is known of their natural history. Because of their extreme rarity, which is a

characteristic of persisters, they might be placed in this category pending further investigation. Of the 25 intertidal species of starfish, five species (20 percent) were characteristic opportunist coral-reef species and 18 species (72 percent) were characteristic persister coral-reef species (stable abundance and size distribution or remained uncommon throughout study). Only two species (8 percent), namely Ophidiaster confertus and Coscinasterias calamaria were sub-tropical, rocky-reef (mainland) species that had extended their ranges to embrace the southernmost reefs of the Great Barrier Reef.

The longevity of a species is determined by the relative probability of juvenile and adult survivorship. In the simplest case, if the probability of a sexually mature organism's survival from one reproductive season to the next is greater than the probability of one of the offspring reaching sexual maturity, then the species will exhibit iteroparity (see Cole, 1954; Murphy, 1968; Goodman, 1974; Stearns, 1977; Roff, 1981; Ebert, 1982). Although neither predation nor mortality was observed during this study, both low adult mortality and relative longevity can be inferred from the stability of the size-frequency distributions of the persistent species studied. This contrasts with the large population fluctuations and instability of the population structure of the opportunist species studied.

Most marine benthic invertebrates have a high energy cost associated with reproduction (Mileikovsky, 1971). Under differing selection pressures, it has been suggested that long life can be associated with either variable recruitment (Sterns, 1977) or fixed low recruitment (Charnov and Schaffer, 1973; Schaffer, 1974; Ebert, 1982). McCallum (1987) and McCallum et al. (1989) have suggested that Acanthaster planci is recruitment limited by juvenile and sub-adult predation.

A model relating to our perception of the life history of all organisms,

referred to as r- versus K- strategy, was reviewed by Stearns (1977). The different survival characteristics in the model were thought to have evolved in response to specific types of environments (Murphy, 1968; Hairston, Tinkle and Wilbur, 1970). The spectrum of existing life history attributes, apparent in any community study (see e.g. Menge, 1975; Vance, 1973), was considered to represent many points on a continuum between the conceptually ideal r- strategists and K-strategists.

It has been suggested that the dispersal stage of a population spreads the risk of local extinction in space and time (Den Boer, 1971; Scheltema, 1971; Strathmann, 1974). Opportunists survive by being able to colonize regions quickly following disturbance. In this regard, an important distinction must be made between equilibrium and non-equilibrium populations in terms of adaptive characteristics (Caswell, 1982; Ebert, 1985). High spatial and temporal variation in population size seems to characterize the typical opportunists.

The degree of spatial and temporal stability in the population of a species determines its position on a theoretical opportunist – persister continuum. Each species was viewed in this context and a basic dichotomy was observed. Because it does not require presumptions of carrying capacity, and inferences about competition, the opportunist / persister model of Endean and Cameron (1990 a) seems to best describe this low density assemblage of coral-reef starfish. Stable ecosystems should be characterized by small fluctuations of their component species. However it is clear that the apparent stability or instability of any biological system is dependent not only on the spatial and temporal scales of observation (Bradbury and Reichelt, 1982; Sale, 1984; Weiss, 1969) but also on the particular subset of species that is examined.

The observed level of numerical and size-frequency stability in the persistent coral-reef asteroid species is consistent with a model of community equilibrium. It is clear that mortality, dispersion, larval survival and settlement phenomena did not result in widely varying size structures or greatly differing adult numbers from one year to the next over a period of 5 years. The vast majority of species of coral-reef starfish in the assemblage studied were characterized by continuing low abundance. It would appear that when a rare, large-bodied starfish is established in its adult population, it is likely to be long lived. Acanthaster planci is a member of this coral-reef starfish assemblage and Cameron (1977) has suggested that only when the coral reef ecosystem is drastically altered can such a rare and long-lived carnivore undergo population outbreaks. This restriction may also apply to other persistent species in the coral-reef starfish assemblage.

Factors such as high gamete dilution (Rothschild and Swann, 1951; Pennington, 1985; Denny and Shibata, 1989; Epel, 1991), as well as basically unpredictable environmental factors such as larval mortality and enormous potential larval dispersion can affect the number of larvae reaching a reef. Because the area of coral reef in the Great Barrier Reef region is relatively small compared with the area of sea surface in the region, the probability of a planktonic starfish larva reaching a coral reef is quite low. Also, if predation on post-settlement juveniles is intense then recruitment will be low. In low density starfish populations, the aggregation of adults prior to spawning may be essential to the reproductive success of a rare species. Because successful recruitment implies that post-settlement juveniles must survive to enter the breeding population, predation on juveniles as well as sub-lethal predation of adults (when loss of gonad affects fecundity) are both forms of recruitment limitation.

The results presented in this study are in accord with the hypothesis of

Endean and Cameron (1990 a) that complex, high diversity assemblages of coral-reef animals are characterized by a predominance of rare, long-lived species with relatively constant population sizes and size structures and a minority of relatively common, short-lived opportunistic species characterized by fluctuating population sizes and size structures.

CHAPTER 11. REFERENCES

Abbott,I. 1983.
The meaning of z in species / area regressions and the study of species turnover in island biogeography. Oikos 41: 385-390.

Achituv,Y. 1972.
The genital cycle of Asterina burtoni Gray [Asteroidea] from the Gulf of Elat, Red Sea. Cah. Biol. Mar. 14(4): 547-553.

Achituv,Y. and Z.Malik. 1985.
The spermatozoa of the fissiparous starfish, Asterina burtoni.
Int. J. Invert. Repro. Devel. 8: 67-72.

Achituv,Y. and E.Sher. 1991.
Sexual reproduction and fission in the sea star Asterina burtoni from the Mediterranean coast of Israel. Bull. mar. sci. 48: 670-678.

Ansell,A.D. 1969.
Defensive adaptations to predation in the mollusca.
Mar. Biol. Assoc. India 3: 487-512.

Antonelli,P.L. and N.D.Kazarinoff. 1988.
Modelling density-dependent aggregation and reproduction in certain terrestrial and marine ecosystems: A comparative study. Ecol. modelling 41: 219-228.

Atkinson,M.J., S.V.Smith and E.D.Stroup, 1982.
Circulation in Enewetak Atoll lagoon.
Proc. 4th Int. Coral Reef Symp. 1: 335-338.

Babcock,R.C. and C.N.Mundy. 1992.
Reproductive biology, spawning and field fertilisation rates of Acanthaster planci. Aust. J. Mar. Freshwater Res. 43: 525-534.

Baker,A.N. and L.M.Marsh. 1974.
The rediscovery of Halityle regularis Fisher [Echinodermata, Asteroidea]. Rec. W.A. Mus. 4(2): 107-116.

Bakus,G.J. 1974.
Toxicity in holothurians: a geographical pattern. Biotropica 6(4): 229-236.

Barker,M.F. 1977.
Observations on the settlement of the brachiolaria larvae of Stichaster australis (Verrill) and Coscinasterias calamaria (Gray) (Echinodermata:

Asteroidea) in the laboratory and on the shore. J. exp. mar. Biol. Ecol. 30: 95-108.

Bennett,I. 1958.
Echinoderms from the Capricorn Group, Queensland, 23-27 S.
Proc. Linn. Soc. N.S.W. 83: 375-376.

Benson,A.A., Patton,J.S. and C.E.Field. 1975.
Wax digestion in the Crown of Thorns starfish.
Comp. Biochem. Physiol. B. Comp. Biochem. 52(2): 339-340.

Benzie,J.A.H. and J.A.Stoddart. 1992.
Genetic structure of outbreaking and non-outbreaking crown-of-thorns starfish (Acanthaster planci) populations on the Great Barrier Reef. Mar. Biol. (Berlin) 112: 119-130.

Benzie,J.A.H. and J.A.Stoddart. 1992.
Genetic structure of crown-of-thorns starfish (Acanthaster planci) in Australia. Mar. Biol. (Berlin) 112: 631-639.

Birkeland,C. 1974.
Interactions between a seapen and seven of its predators.
Ecol. Monogr. 44: 211-232.

Birkeland,C. 1982.
Terrestrial runoff as a cause of outbreaks of Acanthaster planci. Mar. Biol. 69(2): 175-186.

Birkeland,C., Dayton, P.K. and N.A.Engstrom. 1982.
A stable system of predation on a holothurian by four asteroids and their top predator. Aust. Mus. Mem. 16: 175-189.

Black,K.P. 1993.
The relative importance of local retention and inter-reef dispersal of neutrally buoyant material on coral reefs.
Coral reefs 12: 43-53.

Black,K.P. and P.J.Moran. 1991.
Influence of hydrodynamics on the passive dispersal and initial recruitment of larvae of Acanthaster planci (Echinodermata: Asteroidea) on the Great Barrier Reef.
Mar. ecol. prog. ser. 69: 55-65.

Blake,D.B. 1979.
The affinities and origins of the crown-of-thorns sea star Acanthaster

Gervais. J. Nat. Hist. 13: 303-314.

Blake,D.B. 1980.
Affinities of three small sea-star families.
J. Nat. Hist. 14: 163-182.

Blake,D.B. 1981.
A reassessment of the sea-star orders Valvatida and Spinulosida. J. Nat. Hist. 15: 375-394.

Blake,D.B. 1983.
Some biological controls on the distribution of shallow water sea stars (Asteroidea; Echinodermata).
Bull. Mar. Sci. 33: 703-712.

Blake,D.B. 1987.
A classification and phylogeny of post-Paleozoic sea stars (Asteroidea: Echinodermata). J. nat. hist. 21: 481-528.

Blake,D.B. 1990.
Adaptive zones of the class Asteroidea (Echinodermata).
Bull. Mar. Sci. 46: 701-718.

Blankley,W.O. 1984.
Ecology of the starfish Anasterias rupicola at Marion Island (Southern Ocean).
Mar. Ecol. Prog. Ser. 18: 131-138.

Bosch,I. 1989.
Contrasting modes of reproduction in two antarctic asteroids of the genus Porania, with a description of unusual feeding and non-feeding larval types. Biol. Bull. 177: 77-82.

Bosch,I. and J.S.Pearse. 1990.
Developmental types of shallow-water asteroids of McMurdo Sound, Antarctica. Mar. Biol. (Berlin) 104: 41-46.

Bouillon,J. and M.Jangoux. 1985.
Note on the relationship between the parasitic mollusc Thyca crystallina [Gastropoda, Prosobranchia] and the starfish Linckia laevigata [Echinodermata] on Laing Island reef, Papua New-Guineae.
Ann. Soc. R. Zool. Belg. 114(2): 249-256.

Bradbury,R.H. and R.Reichelt. 1982.
The reef and man: Rationalising management through ecological

theory. Proc. 4th Int. Coral Reef Symp.1: 219-223.

Brahimi-Horn,M.C., Guglielmino,M.L., Sparrow,L.G., Logan,R.I. and P.J.Moran. 1989.
Lipolytic enzymes of the digestive organs of the crown-of-thorns starfish (Acanthaster planci): Comparison of the stomach and pyloric caeca. Comp. biochem. physiol. 92: 637-644.

Brown,J.H. 1981.
Two decades of Homage to Santa Rosalia: Towards a theory of diversity. Amer. Zool. 21: 877-888.

Bruno,I., Minale,L., Riccio,R., Cariello,L., Higa,T. and J.Tanaka. 1993.
Starfish saponins: Part 50. Steroidal glycosides from the Okinawan starfish Nardoa tuberculata.
J. natural products 56: 1057-1064.

Bullock,T.H. 1953.
Predator recognition and escape responses of some intertidal gastropods in presence of starfish. Behaviour 5: 130-140.

Burkenroad,M.D. 1957.
Intensity of settling of starfish in Long Island Sound in relationship to fluctuations of the stock of adult starfish and in the settling of oysters. Ecology 38: 164-165.

Cameron,A.M. and R.Endean. 1982.
Renewed population outbreaks of a rare and specialised carnivore (the starfish Acanthaster planci) in a complex high-diversity system (the Great Barrier Reef).
Proc. 4th Int. Coral Reef Symp. 2: 593-596.

Cameron,A.M., Endean,R. and L.M.Devantier. 1991.
Predation on massive corals: Are devastating population outbreaks of Acanthaster planci novel events?
Mar. ecol. prog. ser. 75: 251-258.

Casapullo,A., Finamore,E., Minale,L., Zollo,F., Carre,J.B., Debitus,C., Laurent,D., Folgore,A. and F.Galdiero. 1993.
Starfish saponins: Part 49. New cytotoxic steroidal glycosides from the starfish Fromia monilis. J. natural products 56: 105-115.

Caswell,H. 1982.
Stable population structure and reproductive value for populations with complex life cycles. Ecology 63: 1223-1231.

Chao,S.M. and K.H.Chang. 1989.
Some shallow-water asteroids (Echinodermata: Asteroidea) from Taiwan. Bull. Inst. Zool. Acad. Sinica 28: 215-224.

Charnov,E.L. and W.M.Schaffer. 1973.
Life-History consequences of natural selection: Cole's result revisited. Am. Nat. 107: 791-793.

Chesher,R. 1969 a.
Destruction of Pacific corals by the sea star Acanthaster planci. Science 165: 280-283.

Chesher,R.H. 1969 b.
Acanthaster planci impact on Pacific coral reefs.
Final Rep. Res. Lab. Westinghouse Elect. Corp. to U.S. Dept. Interior, 115 pp.

Christensen,A.M. 1970.
Feeding biology of the sea-star Astropecten irregularis (Pennant). Ophelia 8: 1-134.

Clark,A.H. 1931.
Echinoderms from the islands of Niuafoou and Nukualofa, Tonga Archipelago. Proc. U.S. natn Mus. 80: 1-12.

Clark,A.H. 1952.
Echinoderms from the Marshal Islands.
Proc. U.S. natn Mus. 102: 265-303.

Clark,A.M. 1967 a. Echinoderms from the Red Sea.
Part 2.- Crinoids, Ophiuroids, Echinoids and more Asteroids.
Bull. Sea Fish. Res. Stn Israel. 41: 26-58.

Clark,A.M. 1982.
Echinoderms of Hong Kong.
Proc. Int. Mar. Biol. Workshop 1(1): 485-501.

Clark,A.M. and P.Spencer-Davies. 1966.
Echinoderms of the Maldive Islands.
Ann. Mag. nat. Hist. 13(8): 597-612.

Clark,A.M. and F.W.E.Rowe. 1971.
Monograph of shallow-water Indo-West Pacific Echinoderms. 1-228, pls.1-31, Trustees of the British Museum (Nat. Hist.).

Clark,H.L. 1913.
Autotomy in Linckia. Zool. Anz. 42: 156-159.

Clark,H.L. 1921.
The Echinoderm fauna of Torres Strait. Pap. Dep. Mar. Biol. Carnegie Inst. Wash., 10: viii + 223, pls.1-38.

Clark,H.L. 1938.
Echinoderms from Australia.
Mem. Mus. Comp. Zool. Harv. 55: 1-596.

Clark,H.L. 1946.
The Echinoderm fauna of Australia, its composition and origin.
Carnegie Inst. Wash. 566: 1-567.

Cole,L.C. 1954.
The population consequences of life history phenomena.
Quart. Rev. Biol. 29: 103-137.

Connell,J.H. 1970.
On the role of natural enemies in preventing competitive exclusion in some marine animals and in rainforest trees. in Dynamics of Populations, den Boer,P.J. and G.R.Gradwells (eds): 298-312.

Connell,J.H. 1978.
Diversity in tropical rain forests and coral reefs.
Science 199: 1302-1310.

Connor,E.F. and E.D.McCoy. 1979.
The statistics and biology of the species-area relationship. Am. Nat. 113: 791-833.

Connor,E.F. and D.Simberloff. 1979.
The assembly of species communities; chance or competition? Ecology 60: 1132-1140.

Connor,E.F., E.D.McCoy and B.J.Cosby. 1983.
Model discrimination and expected slope values in species-area studies. Am. Nat. 122: 789-796.

Crump,R.G. and M.F.Barker. 1985.
Sexual and asexual reproduction in geographically separated populations of the fissiparous asteroid Coscinasterias calamaria. J. Exp. Mar. Biol. Ecol. 88: 109-128.

Davis,L.V. 1967.
The suppression of autotomy in Linckia multifora (Lamarck) by the parasitic gastropod, Stylifer linckiae (Sarasin). Veliger 9: 343-346.

Dayton,P.K., R.J.Rosenthal, L.C.Mahan and T.Antezana 1977.
Population structure and foraging biology of the predacious Chilean asteroid Meyenaster gelatinosus and the escape biology of its prey. Mar. Biol. 39: 361-370.

De Celis,A.K. 1980.
The asteroids of Marinduque Island, Philippines.
Acta manil. 19: 20-74.

Den Boer,P.J. 1971.
Stabilization of animal numbers and the heterogeneity of the environment: the problem of the persistence of sparse populations. in Dynamics of Populations, den Boer,P.J. and G.R.Gradwells (eds): 77-97.

Denny,M.W. and M.F.Shibata 1989.
Consequences of surf-zone turbulence for settlement and external fertilisation. Am. Nat. 134: 859-889.

Dight,I.J., Bode,L. and M.K.James. 1990.
Modelling the larval dispersal of Acanthaster planci: I.
Large scale hydrodynamics, Cairns Section, Great Barrier Reef Marine Park (Australia). Coral Reefs 9: 115-123.

Dight,I.J., James,M.K. and L.Bode. 1990.
Modelling the larval dispersal of Acanthaster planci: II.
Patterns of reef connectivity. Coral Reefs 9: 125-134.

Doherty,P.J. 1982.
Coral reef fishes: recruitment-limited assemblages.
Proc. 4th Int. Coral reef Symp. 2: 465-470.

Domantay,J.S. 1972.
Monographic studies and checklist of Philippine littoral Echinoderms.
Acta manil. 15: 91-149.

Dubois,P. and M.Jangoux. 1990.
Stereom morphogenesis and differentiation during regeneration of adambulacral spines of Asterias rubens (Echinodermata, Asteroidea). Zoomorphology (Berlin) 109: 263-272.

Dunbar,M.J. 1960.

The evolution of stability in marine environments: Natural selection at the level of the ecosystem. Am. Nat. 94: 129-136.

Dundar,M.J. 1972.
The ecosystem as unit of natural selection.
Trans. Conn. Acad. Arts Sci. 44: 113-130.

Dunbar,M.J. 1980.
The blunting of Occam's Razor, or to hell with parsimony.
Can. J. Zool. 58: 123-128.

Ebert,T. 1972.
Estimating growth and mortality rates from size data. Oecologia 11(3): 281-298.

Ebert,T. 1982.
Longevity, life history and relative body wall size in sea urchins. Ecol. Monogr. 52: 353-394.

Ebert,T. 1983.
Recruitment in echinoderms. pp 169-203 in Echinoderm Studies vol 1. Lawrence.J and M.Jangoux (eds), A.A.Balkema, Rotterdam.

Ebert,T. 1985.
Sensitivity of fitness to macroparameter changes: an analysis of survivorship and individual growth in sea urchin life histories. Oecologia 65: 461-467.

Eckardt,F.E. 1974.
Life-form, survival strategy and CO2 exchange.
Proc. 1st. Int. Cong. Ecol: 57-59.

Edmondson,C.H. 1935.
Autotomy and regeneration in Hawaiian starfishes.
B.P.Bishop Mus. Occ. Pap. 11(8): 1-29.

Egloff,D.A., Smouse,D.T.Jr. and J.E.Pembroke. 1988.
Penetration of the radial hemal and perihemal systems of Linckia laevigata (Asteroidea) by the proboscis of Thyca crystallina, an ectoparasitic gastropod. Veliger 30: 342-346.

Elder,H.Y. 1979.
Studies on the host parasite relationship between the parasitic prosobranch Thyca crystallina and the asteroid Linckia laevigata. J. Zool. 187(3): 369-392.

Ely,C.A. 1942.
Shallow water Asteroidea and Ophiuroidea of Hawaii.
B.P.Bishop Mus. Bull. 176: 1-163.

Emson,R.H. and I.C.Wilkie. 1980.
Fission and autotomy in echinoderms. Oceanogr. mar. Biol. A. Rev. 18: 155-250.

Endean,R. 1953.
Queensland Faunistic Records Part III. – Echinodermata (excluding Crinoidea). Pap. Dep. Zool. Univ. Qd. 1: 53-60.

Endean,R. 1956.
Queensland Faunistic Records Part IV. – Further records of Echinodermata (excluding Crinoidea). Pap. Dep. Zool. Univ. Qd. 1: 123-140.

Endean,R. 1957.
The biogeography of Queensland's shallow water echinoderm fauna (excluding Crinoidea) with a rearrangement of the faunistic provinces of tropical Australia.
Aust. J. mar. Freshw. Res., 8(3): 233-273.

Endean,R. 1961.
Queensland faunistic records. Part VII. – Additional records of Echinodermata (excluding Crinoidea). Pap. Dep. Zool. Univ. Qd. 1: 289-298.

Endean,R. 1965.
Queensland faunistic records. Part VIII. – Further records of Echinodermata (excluding Crinoidea) from southern Queensland. Pap. Dep. Zool. Univ. Qd. 2: 229-235.

Endean,R. 1969.
Report on investigations made into aspects of the current Acanthaster planci (crown of thorns) infestations on certain reefs of the Great Barrier Reef. Fish. Branch, Qld. Dept. Prim. Ind., Bris. 35 pp.

Endean,R. 1977.
Acanthaster planci infestations of reefs of the Great Barrier Reef. Proc. 3rd Int. Coral Reef Symp. 1: 185-191.

Endean,R. 1982.
Crown-of-thorns starfish on the Great Barrier Reef.
Endeavour 6: 10-14.

Endean,R. and A.M.Cameron. 1990 a.
Trends and new perspectives in coral-reef ecology. pp 469-492 in Ecosystems of the World vol 25, Coral Reefs, Dubinsky,Z. (ed), Elsevier, New York.

Endean,R. and A.M.Cameron. 1990 b.
Acanthaster planci population outbreaks. pp 419-437 in Ecosystems of the World vol 25, Coral Reefs, Dubinsky,Z. (ed), Elsevier, New York.

Epel,D. 1991.
How successful is the fertilisation process of the sea urchin egg. pp 51-54 in Biology of the Echinodermata. Yanagisawa, Yasumasu, Suzuki and Motokawa (eds) Balkema, Rotterdam.

Feder,H.M. 1955.
The use of vital stains in marking Pacific coast starfish.
Calif. Fish. Game 41:245-246.

Feder,H.M. 1963.
Gastropod defensive responses and their effectiveness in reducing predation by starfish. Ecology 44: 505-512.

Fernandes,L. 1990.
Effect of the distribution and density of benthic target organisms on manta tow estimates of their abundance. Coral Reefs 9: 161-165.

Fernandes,L., Marsh,H., Moran,P.J. and D.Sinclair. 1990.
Bias in manta tow surveys of Acanthaster planci. Coral Reefs 9: 155-160.

Fisher,W.K. 1906.
The starfish of the Hawaiian Islands. Bull. U.S. Fish. Commn 23: 987-1130.

Fisher,W.K. 1911.
Asteroidea of the north Pacific and adjacent waters, 1.
Bull. U.S. natn Mus. 76: 1-420.

Fisher,W.K. 1919.
Starfishes of the Philippine Sea and adjacent waters.
Bull. U.S. natn Mus. 100: 1-711.

Fisher,W.K. 1925.
Sea-stars of the tropical central Pacific. B.P.Bishop Mus. Bull. 27: 63-88.

Fisher,R.A., Corbet,A.S. and C.B.Williams. 1943.
The relation between the number of species and the number of individuals in a random sample of an animal population. J. anim. ecol. 12: 42-58.

Fisk,D.A. and V.J.Harriott. 1990.
Spatial and temporal variation in coral recruitment on the Great Barrier Reef (Australia): Implications for dispersal hypotheses. Mar. Biol. (Berlin) 107: 485-490.

Frank,P.W. 1968.
Life histories and community stability. Ecology 49: 355-357.

Frank,P.W. 1969.
Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. Oecologia (Berlin) 2: 232-250.

Franklin,S.E. 1980.
The reproductive biology and some aspects of the population ecology of the holothurians Holothuria leucospilota (Brandt) and Stichopus chloronotus (Brandt). Ph.D. Thesis, University of Sydney.

Gilpin,M.E. and J.M.Diamond. 1982.
Factors contributing to non-randomness in species co-occurrences on islands. Oecologia 52: 75-85.

Gemmill,J.F. 1915.
On the ciliation of asteroids, and on the question of ciliary nutrition in certain species. Proc. zool. Soc. Lond. 1: 1-19.

Gibbs,P.E., C.M.Clark and Clark,A.M. 1976.
Echinoderms from the Great Barrier Reef.
Bull. Br. mus. Nat. Hist. (Zool). 30(4): 103-144.

Glynn,P.W. 1974.
The impact of A. planci on corals and coral reefs in the eastern Pacific. Env. Conserv. 1: 295-304.

Glynn,P.W. 1984.
An amphinomid worm predator of the Crown-of-thorns sea star and general predation on asteroids in eastern and western Pacific coral reefs. Bull. Mar. Sci. 35: 54-71.

Glynn,P.W. and D.A.Krupp. 1986.
Feeding biology of a Hawaiian (USA) sea star corallivore, Culcita

novaeguineae. J. exp. mar. biol. ecol. 96: 75-96.

Goodman,D. 1974.
Natural selection and a cost ceiling on reproductive effort. Am. Nat. 108: 247-268.

Goodman,D. 1975.
The theory of diversity-stability relationships in ecology. Quart. Rev. Biol. 50: 237-266.

Gorshkov,B.A., Gorshkova,I.A., Stonik,V.A. and G.B.Elyakov. 1982.
Effect of marine Glycosides on ATPase activity. Toxicon 20(3): 655-658.

Grassle,J.F. 1973.
Variety in coral reef communities. pp 247-270 in Biology and Geology of Coral Reefs 2, Biology 1, ed. O.A.Jones and R.Endean, New York.

Green,G. 1977.
Ecology of toxicity in marine sponges. Mar. Biol. 40: 207-215.

Grosenbaugh,D.A. 1981.
Qualitative assessment of the Asteroids, Echinoids and Holothurians in Yap Lagoon, West Pacific Ocean. Atoll Res. Bull. 0(254): 49-54.

Guille,A. and M.Jangoux. 1978.
Asterides et Ophiurides littorales de la region d'Amboine (Indonesie). Ann. Inst. oceanogr., Paris. 54(1): 47-74.

Hairston,N.G. 1959.
Species abundance and community organisation. Ecol. 40: 404-416.

Hairston,N.G., D.W.Tinkle and H.M.Wilbur. 1970.
Natural Selection and the parameters of population growth. J. Wildl. Manag. 34: 681-690.

Hayashi,R. 1938 a.
Sea stars of the Ryukyu Islands. Bull. biogr. Soc. Japan. 8: 197-222.

Hayashi,R. 1938 b.
Sea stars of the Ogasawara Islands. Annotnes zool. jap. 17(1): 59-68.

Hayashi,R. 1938 c.
Sea stars of the Caroline Islands. Palau Trop. Biol. Stat. Stud. 3: 417-446.

Hays,J. Imbrie,J. and N.J.Shackleton. 1976.
Variations in the Earth's Orbit: Pacemaker of the Ice Ages. Science 194: 1121-1132.

Henderson,J.A and J.S.Lucas. 1971.
Larval development and metamorphoses of Acanthaster planci (Asteroidea). Nature 232: 655-657.

Hendler,G. 1975.
Adaptational significance of the patterns of ophiuroid development. Amer. Zool. 15: 691-715.

Hurlbert,S.H. 1971.
The non-concept of species diversity.: a critique and alternative parameters. Ecol. 52: 577-586.

Hutchings,P.A. 1981.
Polychaete recruitment onto dead coral substrates at Lizard Island, Great Barrier Reef, Australia. Bull. Mar. Sci. 31: 410-423.

Iorizzi,M., Minale,L., Riccio,R., Higa,T. and J.Tanaka. 1991.
Starfish saponins: Part 46. Steroidal glycosides and polyhydroxysteroids from the starfish Culcita novaeguineae.
J. natural products 54: 1254-1264.

Iwasaki,K. 1993.
Analyses of limpet defence and predator offence in the field.
Mar. Biol. (Berlin) 116: 277-289.

Jacobs,J. 1974.
Diversity, stability and maturity in ecosystems influenced by human activities. Proc. 1st. Int. Cong. Ecol.: 94-95.

Jackson,G.A. and R.R.Strathmann. 1981.
Larval mortality from offshore mixing as a link between precompetent and competent periods of development. Am. Nat. 118: 16-26.

James,D.B. 1972.
Note on the development of the asteroid Asterina burtoni Gray. J. Mar. Biol. Assoc. India 14(2): 883-884.

James,D.B. 1973.
Studies on Indian echinoderms. J. Mar. Biol. Assoc. India 15(2): 556-559.

James,D.B. and J.S.Pearse. 1969.
Echinoderms from the Gulf of Suez and the northern Red Sea.
J. Mar. Biol. Assoc. India 11(1-2): 75-125.

Jangoux,M. 1972 a.
Les asterides de I'lle d'Inhaca (Mozambique) [Echinodermata, Asteroidea]. Annales Mus. r. Afr. cent. (Ser. 8 Sci. Zool.) 208: 1-50.

Jangoux,M. 1972 b.
Le genre Neoferdina Livingstone. Revue Zool. Bot. afr. 87: 775-794.

Jangoux,M. 1978.
Biological results of the Snellius Expedition XXIX. Zool. Medd. 52: 287-300.

Jangoux,M. 1980.
Le genre Leiaster Peters. Rev. Zool. afr. 94: 86-110.

Jangoux, 1982.
Food and feeding mechanisms: Asteroidea. pp 117-159 in Echinoderm Nutrition, Jangoux,M. and J.M.Lawrence (eds), A.A.Balkema, Rotterdam.

Jangoux,M. 1984.
The littoral asteroids from New-Caledonia. Bull. Mus. Natl. Hist. Nat. 6: 279-294.

Jangoux,M. and A.Aziz. 1985.
The asteroids (Echinodermata) of the central-west part of the Indian ocean (Seychelles, Maldive Archipelagoes). Bull. Mus. Nat. Hist. Zool. 6: 857-884.

Jell,J.and P.Flood. 1978.
Guide to the geology of reefs of the Capricorn and Bunker Groups, Great Barrier Reef Province, with special reference to Heron Reef. Pap. Dep. Geol. Univ. Qld. 8: 1-85.

Johnson,C.R., Sutton,D.C., Olson,R.R. and R.Giddins. 1991.
Settlement of crown-of-thorns starfish: Role of bacteria on surfaces of coralline algae and a hypothesis for deepwater recruitment. Mar. ecol. prog. ser. 71: 143-162.

Johnson,M.S. and T.J.Threlfall. 1987.
Fissiparity and population genetics of Coscinasterias calamaria. Mar. Biol. (Berlin) 93: 517-526.

Jost, P. 1979.
Reaction of two sea star species to an artificial prey patch.
Proc. European Colloquium on Echinoderms, Brussels.: 197.

Julka,J.M. and S.Das. 1978.
Studies on the shallow water starfishes of the Andaman and Nicobar Islands. Mitt. Zool. Mus. Berl. 54(2): 345-352.

Kanatani,H. 1969.
Oocyte maturation with 1.Methyl adenine. Expl. Cell. Res. 57: 333-337.

Kanatani,H. 1973.
Maturation-inducing substance in starfishes. Int. Rev. Cytol. 35: 253-298.

Keesing,J.K. and A.R.Halford. 1992.
Field measurement of survival rates of juvenile Acanthaster planci: Techniques and preliminary results. Mar. ecol. prog. ser. 85: 107-114.

Keesing,J.K. and J.S.Lucas 1992.
Field measurement of feeding and movement rates of the crown-of-thorns starfish Acanthaster planci (L.). J. Exp. Mar. Biol. Ecol. 156: 89-104.

Keesing,J.K. and C.M.Cartwright. 1993.
Measuring settlement intensity of echinoderms on coral reefs. Mar. biol. (Berlin) 117: 399-407.

Kenchington,R.A. 1976.
Acanthaster planci on the Great Barrier Reef: detailed surveys of four transects between 19° and 20°S. Biol. Conserv. 9: 165-179.

Kerr,A.M., Norris,D.R., Schupp,P.J., Meyer,K.D., Pitlik,T.J., Hopper,D.R., Chamberlain,J.D. and L.S.Meyer. 1992.
Range extensions of echinoderms (Asteroidea, Echinoidea and Holothuroidea) to Guam, Mariana Islands. Micronesica 25: 201-216.

Kicha,A.A., Kalinovskii,A.I. and E.V.Levina. 1985.
Culcitoside C-1 from the starfishes Culcita novaeguineae and Linckia guildingi. Khimiya Prirodnykh Soedinenii 0 (6): 801-804.

Klopfer,P.H. 1959.
Environmental determinants of faunal diversity. Am. Nat. 93: 337-342.

Klopfer,P.H. and R.H.MacArthur. 1960.

Niche size and faunal diversity. Am. Nat. 94: 293-300.

Klumpp,D.W. and A.Pulfrich. 1989.
Trophic significance of herbivorous macroinvertebrates on the central Great Barrier Reef (Australia). Coral Reefs 8:135-144.

Koehler,R. 1910.
Shallow water Asteroidea. Echinoderms of the Indian Museum 6. Calcutta, 192 pp.

Kohn,A.J. 1959.
The ecology of Conus in Hawaii. Ecol. Monogr. 29: 47-90.

Kohn,A.J. 1968.
Microhabitats, abundance and food of Conus on atoll reefs in the Maldive and Chagos Islands. Ecology 49: 1046-1062.

Kohn,A.J. and P.J.Leviten. 1976.
Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. Oecologia 25: 199-210.

Komatsu,M. 1973.
A preliminary report on the development of the sea-star Leiaster leachi. Proc. Jap. Soc. Syst. Zool. 9: 55-58.

Komatsu,M., Kano,Y.T. and C.Oguro. 1990.
Development of a true ovoviviparous sea star, Asterina pseudoexigua pacifica Hayashi. Biol. Bull. 179: 254-263.

Kuborta,J., Nakao,K., Shirai,H. and H.Kanatani. 1977.
1.Methyl adenine-producing cells in the starfish testes.
Exp. Cell. Res. 106: 63-70.

Kunin,W.E. and K.J.Gaston. 1993.
The biology of rarity: Patterns, causes and consequences. Tree 8(8): 298-301.

Kwon,W.S. and C.H.Cho. 1986.
Culture of the ark shell, Anadara broughtonii in Yoja Bay (Korea). Bull. Korean Fish. Soc. 19: 375-379.

Lawrence,J.M., Klinger,T.S., McClintock,J.B., Watts,S.A., Chen,C.P., Marsh,A. and L.Smith. 1986.
Allocation of nutrient resources to body components by regenerating

(Luidia clathrata) (Echinodermata: Asteroidea).
J. exp. mar. biol. ecol. 102: 47-54.

Laxton, J.H. 1971.
Feeding in some Australian Cymatiidae (Gastropoda: Prosobranchia).
Zool. J. Linn. Soc. 50: 1-9.

Laxton,J.H. 1974.
A preliminary study of the biology and ecology of the blue starfish Linckia laevigata (L) on the Australian Great Barrier Reef and an interpretation of its role in the coral reef ecosystem. Biol. J. Linn. Soc. 6: 47-64.

Leigh,E.G. 1965.
On the relationship between productivity, biomass, diversity, and stability of a community. Proc. Nat. Acad. Sci. 53: 777-783.

Lessios,H.A. 1990.
Adaptation and phylogeny as determinants of egg size in echinoderms from the two sides of the Isthmus of Panama. Am. Nat. 135: 1-13.

Levins,R. and Culver. 1971.
Regional coexistence of species and competition between rare species.
Proc. Nat. Acad. Sci. 68: 1246-1248.

Leviten,P.J. and A.J.Kohn. 1980.
Microhabitat resource use, activity patterns, and episodic catastrophe: Conus on intertidal reef rock benches. Ecol. Monogr. 50: 55-75.

Liao,Y. 1980.
The echinoderms of Xisha Islands, Guangdong Province, China. 4. Asteroidea. Studia Mar. Sin. 17: 153-171.

Livingstone,A.A. 1932.
Asteroidea. Sci. Rept, G.B.R. Exped. 4(8): 241-265.

Loosanoff,V.L. 1937.
Use of Nile Blue Sulphate in marking starfish. Science 85(2208): 412.

Loosanoff,V.L. 1961.
Biology and methods of controlling the starfish, Asterias forbesi.
Fishery Leaflet 520, US Department of Interior, Washington DC.

Loosanoff,V.L. 1964.
Variation in time and intensity of settling of the starfish, Asterias

forbesi, in Long Island Sound during a twenty-five year period. Biol. Bull. 126: 423-439.

Lucas,J. 1984.
Growth, maturation and effects of diet in Acanthaster planci (Asteroidea) and hybrids reared in the laboratory. J. exp. Mar. Biol. Ecol. 79: 129-148.

MacArthur,R.H. 1955.
Fluctuations of animal populations, and a measure of community stability. Ecol. 36: 533-536.

MacArthur,R.H. and R.Levins. 1964.
Competition, habitat selection and character displacement in a patchy environment. Proc. Nat. Acad. Sci. 51: 1207-1210.

Macarthur,R.H. and R.Levins. 1967.
The limiting similarity, convergence and divergence of coexisting species. Am. Nat. 101: 377-385.

Margalef,R. 1963.
On certain unifying principles in ecology. Am. Nat. 97: 357-374.

Margalef,R. 1974.
Diversity, stability and maturity in natural ecosystems.
Proc. 1st. Int. Cong. Ecol.: 66.

Marsh,L.M. 1974.
Shallow-water Asterozoans of southeastern Polynesia
1. Asteroidea. Micronesica 10: 65-104.

Marsh,L.M. 1976.
West Australian Asteroidea since H.L.Clark. Thalassia Jugoslavica 12(1): 213-225.

Marsh,L.M. 1977.
Coral Reef Asteroids of Palau, Caroline Islands. Micronesica 13(2): 251-281.

Marsh,L.M. 1991.
A revision of the echinoderm genus Bunaster (Asteroidea: Ophidiasteridae). Rec. West. Aust. Mus. 51: 419-434.

Martin,T.E. 1981.
Species-area slopes and coefficients: a caution on their interpretation.

Am. Nat. 118: 823-837.

Mauzey,K.P., C.Birkeland and P.K.Dayton 1968.
Feeding behaviour of asteroids and escape responses of their prey in the Puget Sound region. Ecology 49: 603-619.

Maxwell,W.G.H. 1968.
Atlas of the Great Barrier Reef. Elsevier, New York.

May,R.M. 1972.
Will a large complex system be stable? Nature 238: 413-414.

May,R.M. and R.H.MacArthur. 1972.
Niche overlap as a function of environmental variability.
Proc. Nat. Acad. Sci. 69: 1109-1113.

McCallum,H.I. 1987.
Predator regulation of Acanthaster planci.
J. theor. biol. 127: 207-220.

McCallum,H.I., Endean,R. and A.M.Cameron. 1989.
Sublethal damage to Acanthaster planci as an index of predation pressure. Mar. ecol. prog. ser. 56: 29-36.

McClary,D.J. and P.V.Mladenov. 1989.
Reproductive pattern in the brooding and broadcasting sea star Pteraster militaris. Mar. Biol. (Berlin) 103: 531-540.

McClary,D.J. 1990.
Brooding biology of the sea star Pteraster militaris (O.F. Mueller): Energetic and histological evidence for nutrient translocation to brooded juveniles. J. mar. biol. ecol. 142: 183-200.

McEdward,L.R. and F.S.Chia. 1991.
Size and energy content of eggs from echinoderms with pelagic lecithotrophic development. J. exp. mar. biol. ecol. 147: 95-102.

McEdward,L.R. and D.A.Janies. 1993.
Life cycle evolution in asteroids: What is a larva? Biol. Bull. 184: 255-268.

McGuinness,K.A. 1984.
Equations and explanations in the study of species-area curves. Biol. Rev. 59: 423-440.

Mead,A.D. 1900.
On the correlation between growth and food supply in the starfish. Am. Nat. 34: 17-23.

Menge,B.A. 1972 a.
Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. Ecol. Monogr. 42: 25-50.

Menge,B.A. 1972 b.
Competition for food between two intertidal starfish species and its effect on body size and feeding. Ecology 53: 635-644.

Menge,B.A. 1975.
Brood or broadcast? The adaptive significance of different reproductive strategies in two intertidal sea-stars Leptasterias hexactis and Pisaster ochraceus. Mar. Biol. 31: 87-100.

Menge,B.A. 1981.
Effects of feeding on the environment: Asteroidea. pp 521-551 in Echinoderms Nutrition, Jangoux,M. and J.M.Lawrence eds., A.A.Balkema, Rotterdam.

Mileikovsky,S.A. 1971.
Types of larval development in marine bottom invertebrates, their distribution and ecological significance: A reevaluation. Mar. Biol. 10: 193-213.

Miller,R.L. 1989.
Evidence for the presence of sexual pheromones in free-spawning starfish. J. exp. mar. biol. ecol. 130: 205-222.

Minale,L., Pizza,C., Riccio,R., Zollo,F., Pusset,J. and P.Laboute 1984.
Starfish saponins 13. Occurrence of nodososide in the starfish Acanthaster planci and Linckia laevigata. J. Nat. Prod. 47(3): 558.

Minchin,D. 1987.
Sea-water temperature and spawning behavior in the sea star Marthasterias glacialis. Mar. Biol. (Berlin) 95: 139-144.

Miyazawa,K., Noguchi,T., Maruyama,J., Jeon,J.K., Otsuka,M. and K.Hashimoto. 1985.
Occurrence of tetrodotoxin in the starfishes Astropecten polyacanthus and Astropecten scoparius in the Seto Inland Sea. Mar. Biol. (Berlin) 90: 61-64.

Miyazawa,K., Higashiyama,M., Hori,K., Noguchi,T., Ito,K. and K.Hashimoto. 1987.
Distribution of tetrodotoxin in various organs of the starfish Astropecten polyacanthus. Mar. Biol. (Berlin) 96: 385-390.

Mladenov,P.V. and R.H.Emson. 1984.
Divide and broadcast: Sexual reproduction in the West Indian brittle star Ophiocomella ophiactoides and its relationship to fissiparity. Mar. Biol. (Berlin) 81: 273-282.

Mladenov,P.V., Carson,S.F. and C.W.Walker. 1986.
Reproductive ecology of an obligately fissiparous population of the sea star Stephanasterias albula. J. exp. mar. biol. ecol. 96: 155-176.

Mladenov,P.V., Bisgrove,B., Asotra,S. and R.D.Burke. 1989.
Mechanisms of arm-tip regeneration in the sea star, Leptasterias hexactis. Roux's arch. devel. biol. 198: 19-28.

Mladenov,P.V. and R.H.Emson. 1990.
Genetic structure of populations of two closely related brittle stars with contrasting sexual and asexual life histories, with observations on the genetic structure of a second asexual species. Mar. Biol. (Berl) 104: 265-274.

Moran, P. 1986.
The Acanthaster phenomenon.
Oceanogr. Mar. Biol. Ann. Rev. 24: 379-480.

Moran,P.J. and G.De'ath. 1992 a.
Estimates of the abundance of the crown-of-thorns starfish Acanthaster planci in outbreaking and non-outbreaking population on reefs within the Great Barrier Reef. Mar. biol. (Berlin) 113: 509-515.

Moran,P.J. and G.De'ath. 1992 b.
Suitability of the manta tow technique for estimating relative and absolute abundances of crown-of-thorns starfish (Acanthaster planci L.) and corals. Aust. J. mar. freshw. res. 43(2): 357-378.

Morse,D.E. 1984.
Biochemical control of larval recruitment and marine fouling.
pp 134-141 in Marine Biodeterioration: An Interdisciplinary Study. Costlow,J.D. and R.C.Tipper eds., Naval Inst. Press, Annapolis, Maryland.

Mortensen,T. 1937.

Contributions to the study of the development and larval forms of echinoderms. III.
K. danske Vidensk. Selsk. Skr. 9 Raekke 7(1): 1-65.

Mortensen,T. 1938.
Contributions to the study of the development and larval forms of echinoderms. IV.
K. danske Vidensk. Selsk. Skr. 9 Raekke 7(3): 1-59.

Mortensen,T. 1940.
Echinoderms from the Iranian Gulf. Asteroidea.
Dan. scient. Invest. Iran. 2: 55-110.

Muenchow,G. 1978.
A note on the timing of sex in asexual/sexual organisms. Am. Nat. 112: 774-779.

Murphy,G.I. 1968.
Pattern in life-history and the environment. Am. Nat. 102: 391-411.

Narita,H., Nara,M., Baba,K., Ohgami,H., T.K.Ai., Noguchi,T. and K.Hashimoto. 1984.
Effect of feeding a trumpet shell, Charonia sauliae with toxic starfish (Astropecten polyacanthus). J. Food Hygienic Soc. Japan 25: 251-255.

Nash,W.J., Goddard,M. and J.S.Lucas. 1988.
Population genetic studies of the crown-of-thorns starfish, Acanthaster planci (L.), in the Great Barrier Reef region (Australia).
Coral Reefs 7: 11-18.

Newell,N.D. 1972.
The evolution of reefs. Sci. Am. 226 (6): 54-65.

Nishida,M. and J.S.Lucas. 1988.
Genetic differences between geographic populations of the crown-of-thorns starfish throughout the Pacific region. Mar. Biol. (Berlin) 98: 359-368.

Noguchi et al. 1982.
Tetrodotoxin in the starfish Astropecten polyacanthus in association with toxification of a trumpet shell, “Boshubora” Charonia sauliae.
Bull. Jap. Soc. Sci. Fish. 48: 1173-1177.

Noguchi,T., Sakai,T., Maruyama,J., Jeon,J.K., Kesamaru,K. and K.Hashimotu. 1985 a.

Toxicity of a trumpet shell, Charonia sauliae ("Boshubora") inhabiting along the coasts of Miyazaki Prefecture (Japan). Bull. Jap. Soc. Scient. Fish. 51: 677-680.

Noguchi,T., Jeon,J.K., Maruyama,J., Sato,Y., Saisho,T. and K.Hashimoto. 1985 b.
Toxicity of trumpet shells inhabiting the coastal waters of Kagoshima prefecture (Japan) along with identification of the responsible toxin. Bull. Jap. Soc. Scient. Fish. 51: 1727-1732.

Nojima,S., Soliman,F.E.S., Kondo,Y., Kuwano,Y., Nasu,K. and C. Kitajima. 1986.
Some notes on the outbreak of the sea star, Asterias amurensis versicolor, in the Ariake Sea, western Kyushu (Japan). Pub. Amakusa Mar. Biol. Lab. 8: 89-112.

Oguro,C. 1984.
Supplementary notes on the sea-stars from the Palau and Yap Islands 1. Annot. Zool. Jpn 56(3): 221-226.

Oguro,C., Komatsu,M. and Y.T.Kano. 1975.
A note on the early development of Astropecten polyacanthus (M&T). Proc. Jap. Soc. Syst. Zool. 11: 49-52.

Okaji,K. 1991.
Delayed spawning activity in dispersed individuals of Acanthaster planci in Okinawa. pp 291-295 in Biology of the Echinodermata. Yanagisawa, Yasumasu, Suzuki and Motokawa (eds) Balkema, Rotterdam.

Olsen,R.R. 1987.
In situ culturing as a test of the larval starvation hypothesis for the crown-of-thorns starfish, Acanthaster planci. Limnol. oceanogr. 32: 895-904.

Ormond, R.F.G. and A.C.Campbell. 1973.
Formation and breakdown of Acanthaster planci aggregations in the Red Sea. Proc. 2nd Int. Coral Reef Symp. 1: 595-619.

Ormond,R.F.G., N.J.Hanscomb and D.H.Beach. 1976.
Food selection and learning in the crown-of-thorns starfish, Acanthaster planci. Mar. Behav. Physiol. 4(2): 93-105.

Ottesen,P.O. and J.S.Lucas. 1982.
Divide or Broadcast: Interrelation of Asexual and Sexual Reproduction

in a Population of the Fissiparous Hermaphroditic Seastar Nepanthia belcheri (Asteroidea: Asterinidae). Mar. Biol. 69: 223-233.

Patton,M.L., Brown,S.T., Harman,R.F. and R.S.Grove. 1991.
Effect of the anemone Corynactis californica on subtidal predation by sea stars in the southern California Bight (USA). Bull. mar. sci. 48: 623-634.

Pearse,J.S. 1968.
Patterns of reproductive periodicities in four species of Indo-Pacific echinoderms. Proc. Indian Acad. Sci. 67: 247-279.

Pearse,J.S. 1970.
Reproductive periodicities if Indo-Pacific invertebrates in the Gulf of Suez. 3. The echinoid Diadema setosum (Leske). Bull. Mar. Sci. 20: 697-720.

Pearse,J.S. 1975.
Lunar reproductive rhythms in sea urchins.
A review. J. Interdiscipl. Cycle Res. 6: 47-52.

Pearson,R.G. and R.Endean. 1969.
A preliminary study of the coral predator Acanthaster planci (L.) (Asteroidea) on the Great Barrier Reef. Fisheries Notes Qld. Dept. Harbours and Marine, Brisbane 3: 27-55.

Pennington, J.T. 1985.
The ecology of fertilisation of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. Biol. Bull. 169: 417-430.

Percharde, P.L. 1972.
Observations on the gastropod Charonia variegata, in Trinidad and Tobago. Nautilus, Philad. 85: 84-92.

Peters,R.H. 1976.
Tautology in evolution and ecology. Am. Nat. 110: 1-12.

Phillips,D.W. 1976.
The effect of a species-specific avoidance response to predatory starfish on the intertidal distribution of two gastropods. Oecologia (Berlin) 23: 83-94.

Pianka,E.R. 1966.
Latitudinal gradients in species diversity: a review of concepts. Am.

Nat. 100: 33-46.

Pianka,E.R. 1972.
r- and K- selection or b- and d- selection? Am. Nat. 106: 581-588.

Pielou,E.C. 1981.
The usefulness of ecological models: A stocktaking. Quart. Rev. Biol. 56: 17-31.

Pimm,S.L. 1984.
The complexity and stability of ecosystems. Nature 307: 321-326.

Pope,E.C. and F.W.E.Rowe. 1977.
A new genus and two new species in the family Mithrodiidae [Echinodermata, Asteroidea] with comments on the status of the Mithrodia species. Aust. Zool. 19: 201-216.

Price,A.R.G. 1981.
Echinoderm fauna of the western Arabian Gulf. J. Nat. Hist. 15: 1-16.

Price,A.R.G. 1982.
Western Arabian Gulf echinoderms in high salinity waters and the occurrence of dwarfism. J. Nat Hist. 16(4): 519-528.

Quinn,J.F. and A.E.Dunham. 1983.
On hypothesis testing in ecology and evolution. Am. Nat. 122: 602-617.

Reichelt,R.E. 1982.
Space: A non-limiting resource in the niches of some abundant coral reef gastropods. Coral Reefs 1: 3-11.

Ribi, G. and P.Jost, 1978.
Feeding rate and duration of daily activity of Astropecten aranciacus (Echinodermata: Asteroidea) in relation to prey density. Marine Biology 45: 249-254.

Riccio,R., Dini,A., Minale,L., Pizza,C., Zollo,F. and T.Sevenet 1982.
Starfish saponins VII. Structure of luzonicoside, a further steroidal cyclic glycoside from the Pacific starfish Echinaster luzonicus. Experimentia (Basel) 38: 68-70.

Riccio,R., Greco,O.S., Minale,L., Pusset,J. and J.L.Menou 1985. Starfish saponins 18. Steroidal glycoside sulphates from the starfish Linckia laevigata.

J. Nat. Prod. 48(1): 97-101.

Rideout,R.S. 1975.
Toxicity of the asteroid Linckia laevigata (L.) to the damselfish Dascyllus aruanus (L.). Micronesica 11(1): 153-154.

Rideout,R.S. 1978. Asexual reproduction as a means of population maintenance in the coral reef asteroid Linckia multifora on Guam. Mar. Biol. 47(3): 287-296.

Roff,D.A. 1981.
Reproductive uncertainty and the evolution of iteroparity: Why don't flatfish put all their eggs in one basket? Can. J. Fish. aquat. Sci. 38: 968-977.

Rothschild,Lord and M.M.Swann. 1951.
The fertilisation reaction in the sea urchin. The probability of a successful sperm-egg collision. J. exp. biol. 28: 403-416.

Roughgarden,J. 1983.
Competition and theory in community ecology. Am. Nat. 122: 583-601.

Rowe,F.W.E. 1977.
The status of Nardoa subgenus Andora [Asteroidea, Ophidiasteridae] with the description of 2 new subgenera and 3 new species. Rec. Aust. Mus. 31(6): 235-244.

Run,J.Q., Chen,C.P., Chang,K.H. and F.S.Chia. 1988.
Mating behavior and reproductive cycle of Archaster typicus (Echinodermata: Asteroidea). Mar. Biol. (Berl) 99: 247-254.

Sale,P.F. 1974.
Mechanisms of co-existence in a guild of territorial fishes at Heron Island. Proc. 2nd Int. Coral reef Symp. 1: 193-206.

Sale,P.F. 1976.
Reef fish lottery. Nat. Hist. 85: 60-65.

Sale,P.F. 1977.
Maintenance of high diversity in coral reef fish communities. Am. Nat. 111: 337-359.

Sale,P.F. 1984.
The structure of communities of fish on coral reefs and the merit of a

hypothesis testing, manipulative approach to ecology. in Ecological Communities: Conceptual issues and the evidence. pp 478-490. ed. D.Strong, D.Simberloff, L.Abele and A.Thistle. Princeton Univ. Press, Princeton, N.J.

Sale,P.F. 1991.
Reef fish communities: open nonequilibrial systems. pp 564-598 in The ecology of fishes on coral reefs. P.F.Sale. (ed) Academic Press, San Diego.

Sale,P.F. and R.Dybdahl. 1975.
Determinants of community structure for coral reef fishes in an experimental habitat. Ecology 56: 1343-1355.

Sale,P.F. and W.A.Douglas. 1984.
Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. Ecology 65: 409-422.

Schaffer,W.M. 1974.
Optimal reproductive effort in fluctuating environments. Am. Nat. 108: 783-790.

Scheibling,R.E. 1980.
Dynamics and feeding activity of high-density aggregations of Oreaster reticulatus (Echinodermata: Asteroidea) in a sand patch habitat. Mar. Ecol. Prog. Ser. 2: 321-327.

Scheibling,R.E. 1981 a.
Growth and respiration rate of juvenile Oreaster reticulatus (L.) (Echinodermata: Asteroidea) on fish and algal diets.
Comp. Biochem. Physiol. 69A: 175-176.

Scheibling,R.E. 1981 b.
Optimal foraging movements of Oreaster reticulatis (L) (Echinodermata: Asteroidea). J. Exp. Mar. Biol. Ecol. 51: 173-185.

Scheibling,R.E. 1982.
Feeding habits of Oreaster reticulatus (Echinodermata: Asteroidea). Bull. Mar. Sci. 32: 504-510.

Scheltema,R.S. 1968.
Dispersal of larvae by equatorial ocean currents and its importance to the zoogeography of shoal-water tropical species. Nature 217: 1159-1162.

Scheltema,R.S. 1971.
Larval dispersal as a means of genetic exchange between geographically separated populations of shallow water benthic marine gastropods. Biol. Bull. 140: 284-322.

Schmitt,R.J. 1982.
Consequences of dissimilar defences against predation in a subtidal marine community. Ecology 63: 1588-1601.

Shiomi,K., Yamamoto,S., Yamanaka,H. and T.Kikuchi. 1988.
Purification and characterization of a lethal factor in venom from the crown-of-thorns starfish (Acanthaster planci). Toxicon 26: 1077-1084.

Shiomi,K., Yamamoto,S., Yamanaka,H., Kikuchi,T. and K.Konno. 1990.
Liver damage by the crown-of-thorns starfish (Acanthaster planci) lethal factor. Toxicon 28: 469-476.

Slattery,M. and I.Bosch. 1993.
Mating behavior of a brooding Antarctic asteroid, Neosmilaster georgianus. Invert. repro. devel. 24: 97-102.

Sloan,N.A. 1980.
Aspects of the feeding biology of asteroids.
Oceanogr. mar. Biol. ann. Rev. 18: 57-124.

Stearns,S.C. 1977.
Life history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3-47.

Stevenson,J.P. 1992.
A possible modification of the distribution of the intertidal seastar Patiriella exigua (Lamarck) (Echinodermata: Asteroidea) by Patiriella calcar (Lamarck). J. exp. mar. biol. ecol. 155: 41-54.

Strathmann,R.R. 1974.
The spread of sibling larvae of sedentary marine invertebrates. Am. Nat. 108: 29-44.

Strathmann,R.R. 1978.
The evolution and loss of feeding larval stages of marine invertebrates. Evolution 32: 894-906.

Strathmann,R.R. and K.Vedder. 1977.
Size and organic content of eggs of echinoderms and other invertebrates as related to developmental strategies and egg eating. Mar. Biol. 39(4): 305-309.

Strong,R.D. 1975.
Distribution, morphometry, and thermal stress studies on two forms of Linckia (Asteroidea) on Guam. Micronesica 11: 167-183.

Stump,R.J.W. and J.S.Lucas. 1990.
Linear growth in spines from Acanthaster planci (L.) involving growth lines and periodic pigment bands. Coral Reefs 9: 149-154.

Sughihara,G. 1981.
S=CAZ, Z=1/4: a reply to Connor and McCoy. Am. Nat. 117: 790-793.

Talbot,F.H., Russell,B.C. and G.R.V.Anderson. 1978.
Coral reef fish communities: unstable high-diversity systems?
Ecol. monogr. 48: 425-440.

Thandar,A.S. 1989.
Zoogeography of the southern African echinoderm fauna.
South Afr. J. zool. 24: 311-318.

Thomassin,B.A. 1976.
The feeding behaviour of the felt-, sponge-, and coral- feeding sea stars, mainly Culcita schmideliana. Helg. wiss. Meeres. 28: 51-65.

Thompson,G.B. and C.Thompson. 1982.
Movement and size structure in a population of the blue starfish Linckia laevigata (L.) at Lizard Island, Great Barrier Reef. Aust. J. Mar. Freshw. Res. 33: 561-573.

Thorson,G. 1950.
Reproductive and larval ecology of marine invertebrates. Biol. Rev. 25: 1-45.

Thorson,G. 1966.
Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea. Res. 3: 267-293.

Tokeshi,M. 1991.
Extraoral and intraoral feeding: Flexible foraging tactics in the South American sun-star, Heliaster helianthus. J. zool. (London) 225: 439-448.

Tortonese,E. 1960.
Echinoderms from the Red Sea. 1. Asteroidea.
Bull. Sea. Fish. Res. Stn. Israel 29: 17-23.

Tortonese,E. 1977.
Report on echinoderms from the Gulf of Aqaba (Red Sea).
Monit. Zool. Ital. Suppl. 9 (12): 273-290.

Tortonese,E. 1979.
Echinoderms collected along the eastern shore of the Red Sea. Atti.
Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano 120: 314-319.

Tortonese,E. 1980.
Researches on the coast of Somalia: Littoral Echinodermata.
Monit. Zool. Ital. Suppl. 13(5): 99-140.

Turner,R.L. 1976.
Sexual difference in latent period of spawning following injection of the hormone 1. Methyl adenine in Echinaster (Echinodermata: Asteroidea).
General comp. Endocr. 28: 109-112.

Vance,R.R. 1973.
On reproductive strategies in marine benthic invertebrates.
Am. Nat. 107: 339-352 and 353-361.

Vermeij,G.J. 1987.
Evolution and escalation. Princeton Univ. Press, Princeton, New Jersey. 528pp.

Vernon,A.A. 1937.
Starfish stains. Science 86: 64.

Walenkamp,J.H.C. 1990.
Systematics and zoogeography of Asteroidea (Echinodermata) from Inhaca Island, Mozambique. Zool. Verh. 0(261): 3-86.

Weiss,P. 1969.
This living system: determination stratified. pp 3-53 in Beyond Reductionism. Koestler,A. and A.Smythies (eds), Hutchinson, London.

Williams,S.T. and J.A.H.Benzie. 1993.
Genetic consequences of long larval life in the starfish Linckia laevigata (Echinodermata: Asteroidea) on the Great Barrier Reef. Mar. Biol. (Berlin) 117: 71-77.

Wolanski,E. 1993.
Facts and numerical artefacts in modelling the dispersal of crown-of-thorns starfish larvae in the Great Barrier Reef. Aust. J. mar. freshw.

res. 44: 427-436.

Wolda,H. 1970.
Ecological variation and its implications for the dynamics of populations of the land snail Cepacea nemoralis. pp 98-108 in Dynamics of Populations. den Boer,P.J. and G.R.Gradwells (eds), Centre for Agricultural Publishing and Documentation, Wageningen.

Yamaguchi,M. 1973 a.
Recruitment of coral reef asteroids, with emphasis on Acanthaster planci. Micronesica 9: 207-212.

Yamaguchi,M. 1973 b.
Early life histories of coral reef asteroids, with special reference to Acanthaster planci. pp 369-387 in Biology and Geology of Coral Reefs, 2. Biol 1. O.A.Jones and R.Endean (eds), Academic Press, New York.

Yamaguchi,M. 1974.
Larval life span of the coral reef asteroid Gomophia egyptiaca (Gray). Micronesica 10: 57-64.

Yamaguchi,M. 1975 a.
Estimating growth parameters from growth data. Oecologia (Berlin) 20: 321-332.

Yamaguchi,M. 1975 b.
Coral reef asteroids of Guam. Biotropica 7: 12-23.

Yamaguchi,M. 1977 a.
Population structure, spawning, and growth of the coral reef asteroid Linckia laevigata (Linnaeus). Pac. Sci. 31: 1330.

Yamaguchi,M. 1977 b.
Larval behaviour and geographic distribution of coral reef asteroids in the Indo-West Pacific. Micronesica 13: 283-296.

Yamaguchi,M. 1977 c.
Estimating the length of the exponential growth phase growth increment observations on the coral reef asteroid Culcita novaeguineae. Mar. Biol. 39: 57-60.

Yamaguchi,M. and J.S.Lucas. 1984.
Natural parthenogenesis, larval and juvenile development, and geographical distribution of the coral reef asteroid Ophidiaster granifer. Mar. Biol. 83: 33-42.

Zagalsky,P.F., Haxo,F., Hertzberg,S. and S.Liaaen-Jensen. 1989. Studies on a blue carotenoprotein, linckiacyanin, isolated from the starfish Linckia laevigata (Echinodermata: Asteroidea). Comp. biochem. physiol. 93: 339-354.

Zann,L., Brodie,J., Berryman,C. and M.Naqasima. 1987. Recruitment, ecology, growth and behavior of juvenile Acanthaster planci (L.) (Echinodermata: Asteroidea). Bull. Mar. Sci. 41: 561-575.

APPENDIX

Sometimes, it is not easy to put a story into words. I often wish that there was a ghost-writer as it is not as simple as just writing the thoughts down. Talking about ideas is one thing, but when written, it is totally different. I have tried that, and it has been life changing to say the least. Have you ever wished that you could have expressed something in a much better manner? Certainly, but sometimes things simply must be said. When it comes to writing, we get the chance to edit our thoughts but that does not necessarily solve the problem Often, people don't want to hear or read things and we feel that silence is not an option.

This was my situation many years ago in 1984. Having just read the novel, I was acutely aware of the silence problem and perhaps like Winston in the book, I felt that I had to do something about it irrespective of the consequences. I had been studying coral-reef starfish for many years at the University of Queensland and together with my academic supervisor Dr Robert Endean and co-supervisor Dr Ann Cameron, we believed that the role of natural predators such as fish and the giant triton in mitigating outbreaks of the crown-of-thorns starfish had not been adequately investigated.

Unfortunately, during 5 years of both intertidal and subtidal sampling at Heron Island, which is towards the southern end of the Great Barrier Reef, I had not observed any predation events on starfish nor located any specimens of the giant triton. Heron Island also had not experienced any outbreaks of crown-of-thorns starfish despite their occurrence on several reefs further south.

I finally wrote up my Doctor of Philosophy thesis intitled "Life-History Strategies of Coral-Reef Asteroids" and it was submitted for examination in December 1985. The internal examination was prompt and favourable, but there was a considerable delay of many months in the return of the overseas examiners' reports. Meanwhile, I was employed mid-July 1986 by the University of Queensland studying starfish predators before the external examiners' reports were received by the university. Although the external examiners' comments were directed at my general failure to clearly state the thesis that was being defended, the thesis contained several unacceptable suggestions.

> "Juveniles of the common, sexually reproducing, large-bodied asteroids .... were rare and the populations of these species were adult dominated throughout the study period".

> "Considering the high reproductive effort displayed by most of the common species, there is little evidence of successful recruitment. It is possible, when the population is at low density, that many eggs are never fertilised".

My employment by the University of Queensland on this starfish predator project was under a consultancy agreement between Uniquest and the Great Barrier Reef Marine Park Authority (GBRMPA). A condition of the agreement was that I should have a doctoral degree for the position, but the examiners first required a revision and resubmission of the thesis. Fortunately, or unfortunately, depending on how one looks at it, the first 2 weeks of my employment on this project changed everything when several giant tritons, some feeding on starfish, were discovered.

In those 2 weeks, together with 20 Australian navy divers, we located 12 giant tritons during a starfish control program conducted by GBRMPA at Grub Reef off Townsville. It was obvious that the giant triton was much more likely to be encountered by divers on a reef that was undergoing a starfish population outbreak, particularly if starfish were being killed during a control program. It was also obvious that the giant triton generated an alarm response and avoidance behaviour in the crown-of-thorns starfish. This made testing of the Predator Control Hypothesis (the subject of the consultancy research) very difficult and was summarized in my progress report to the University:

“The attack of the triton elicits an escape response by the starfish which, if successful, results in rapid prey dispersion with the loss of only a few arms. The escape response varies in its successfulness and is heavily dependent on (1) size and hunger of predator, (2) prey size and degree of cumulative prey injury and (3) physical composition and relief of substrate. If the escape response is unsuccessful then the predator feeds on the starfish until the prey is either consumed (large predator-small prey) or discarded (small predator-large prey). Charonia tritonis will follow the scent of an injured starfish and resume the attack and subsequent feeding if hungry. When not in the process of prey hunting, capture or feeding, Charonia tritonis can appear inert. Under turbulent water-current conditions, the sensitive olfactory organ of Charonia tritonis can be disabled temporarily giving the appearance of random searching behaviour.

The distance over which Charonia tritonis can locate an uninjured prey by chemo-detection is unknown, but the osphradium (olfactory organ) is most highly developed in the Cymatiidae which actively hunt their prey or scavenge dead animals (Morton, 1958). If an Acanthaster

is injured, Charonia is certainly capable of small-scale chemical prey location, but the distance over which this is effective is unknown also. When either one of the two sensory tentacles of Charonia has touched the spine of a large specimen of Acanthaster, the gastropod raises the anterior region of the foot sufficiently high above the substrate to allow it to pass over the spines of the closest three arms of the starfish. When this has occurred, the proboscis of the gastropod is extended and as the foot descends on the aboral surface of the starfish, the proboscis probes the surface between the spines, in an orderly manner, and subsequently extends in excess of 250mm as it reaches over the aboral surface and back under the oral surface while the proboscis tip attempts to penetrate the heavily armoured mouth of the starfish. This is achieved by a combination of physical radula abrasion and chemical attack.

Although specimens of the asteroid Choriaster granulosa are immobilized following direct body wall proboscis penetration, Charonia seems incapable of penetrating the body wall of a complete Acanthaster planci. When specimens of Linckia laevigata, Gomophia sp. and juveniles of Acanthaster planci are attacked, the proboscis extends sufficient to overturn the specimen into the upturned anterior region of the gastropod's foot. The engulphed asteroid is held in this manner while consumed.

The sensory tentacles at the tip of each arm of Acanthaster planci can detect the presence of Charonia tritonis. When one of these tentacles touches the foot of the gastropod, the starfish immediately moves rapidly to avoid capture. If the gastropod has its foot holding the starfish by its arms, these will be autotomized almost immediately to allow escape. If the gastropod has been able to grasp more than a few arms with its foot, then it will use the highly toothed lip of the shell to further restrain the starfish while the proboscis attempts to penetrate the oral spines. The starfish will attempt to escape by crawling laterally over the shell of the gastropod. This causes the gastropod to fall on its side and if the penetration of the starfish's oral spines has not been achieved then escape is often successful. By this time, much damage has already been caused to the oral spines which will make future predator attack more successful.

The structural complexity of external spinulation inhibits, to varying degrees, the proboscis penetration by gastropod predators and parasites. Thickness of test, toxin, and venom elaboration, along with the spatial organization of papular groups probably serve a similar purpose. The usefulness of these structures is apparent following careful examination of the method of predator attack. These defences

maximize the probability of prey escape by increasing the time necessary for the predator to immobilize its prey.

In Trinidad during February large numbers of the asteroid Echinaster sentus congregate in sheltered areas to spawn. Percharde (1972) describes pairs of Charonia tritonis variegata methodically driving dozens of Echinaster sentus up a slope, attacking the outside members. He proposes that this mollusc plays an important role in the ecological balance of the extensive areas of its habitat.

Field and aquarium behavioural observations suggest that Charonia tritonis can disperse aggregations of Acanthaster planci. The reproductive success of Acanthaster planci is heavily dependent on the proximity of conspecifics during spawning. Charonia tritonis may play an important role in the dispersion of both feeding and breeding aggregations of Acanthaster planci."

…. End of progress report (Report to GBRMPA 1986)

I was told that the consultancy agreement required extensive surveying of multiple reefs for general starfish predators, not limited just to the giant triton. I explained that because the giant triton and possibly other generalist predators were attracted to starfish outbreaks, there would not be a simple inverse correlation between predators and starfish, which was the prediction of the hypothesis that was being field tested.
I was also told that any new data relating to starfish predation by the giant triton could not be incorporated into my revised thesis because the data was obtained after the original submission of the thesis. Given this ultimatum by the university, what was I to do? Even though I thought that it was unreasonable and scientifically unjustifiable, that was the university's thesis rules, and they couldn't make an exception just for me.

On further reconsideration, I suggested getting more data which turned out to be a much better scientific solution, particularly considering the limited funds and logistical support that was available for the project. The consultancy continued without my participation for another 6 months while I followed up on ideas relating to the dispersal of starfish aggregations by the giant triton. The university and my supervisor were not very happy, and my doctoral thesis was on hold and ended up not being resubmitted for another 8 years. By this time my supervisor had retired.

During this intervening period, further surveys for giant triton were conducted on John Brewer Reef off Townsville (Report to GBRMPA

1988) and Norman, Hastings, and Saxon Reefs off Cairns (Report to GBRMPA 1990). An attempt was made to publish the results in a scientific journal but unfortunately it was not accepted for publication. This extremely difficult and controversial scientific and employment issue was also extensively considered by Justice Barry, a Presidential Member of the Administrative Appeals Tribunal in the case of Paterson v Secretary, Department of Social Security (DSS) in 1990. Needless-to-say, the university, my supervisor, the GBRMPA and DSS were not very happy with the result following its publication in the media in 1990 and again in 1992.

By 1993, it was apparent that something had to be done regarding revision of the thesis. The first step was an informal Freedom of Information request with the University of Queensland. Unfortunately, my file seemed to have gone missing from the Zoology Department records. It was found to have slipped behind other files when a formal request was subsequently made. The request was further extended to include material in the university's archive. This provided information on the examiners' reports, as well as communications within the university. With this information, submissions were made to Professor Siddle, the Dean of the Post-Graduate Studies Committee:

21 December 1993,
Professor David Siddle
Dean, Postgraduate Studies
University of Queensland

Dear Professor Siddle,
Thank-you for your letter of 30 November offering to have the matter of revision and re-submission of my thesis discussed at the first meeting of the Postgraduate Research Studies Committee in 1994. I give my full and specific approval to discussion of this matter by the Committee and would add that I am prepared to attend and answer any questions relating to either the thesis, the UNIQUEST consultancy or the delay in re-submission if the Committee feels that this would be of assistance in their discussion.

At the beginning of this year, Dr Greenwood had told me that he was willing to supervise this project if no other supervision was available, but Professor Grigg and Dr Johnson have stated that they did not consider him to be suitable. While I accept Dr Johnson's refusal to supervise the project himself, and I thank him for giving it his consideration, I personally feel that Dr Greenwood would have been an excellent supervisor considering both his general knowledge of marine science and his familiarity with my situation.

As the Committee may be aware, supervision difficulties have precluded revision and resubmission of my thesis for a long time and, as Professor Kikkawa will confirm, these began immediately prior to submission when he had to direct Dr Endean that a supervisor's permission is not required for submission of a thesis. This difficult situation deteriorated further during the UNIQUEST consultancy when Dr Endean and I came into direct conflict over methods. I should stress however that I am in complete agreement with Dr Endean's finding that humans caused the starfish outbreaks and in particular, I fully support his earliest proposition regarding collection by humans of the Giant Triton shell.

Given that no supervisor is available for the extended project and given that you do not consider the award of a Masters degree to be appropriate, I request permission to revise and re-submit the original thesis, with or without supervision. I do feel however, that a suitable and willing supervisor could now be found for the limited purpose of thesis revision and re-submission, as distinct from your previous suggestion of a new project incorporating much of the old thesis. I am sure that submission can be accomplished without delay if the Committee will approve this course of action.

From 1987 to 1993, I made several informal approaches to academic staff members of the Zoology Department regarding supervision, but an encouraging response was not received until early 1993. Throughout this period, research funds were sought also from the Great Barrier Reef Marine Park Authority (GBRMPA) to clarify specific points relating to predatory regulation of starfish numbers that were relevant to the revision of my thesis. One such proposal was funded and in April 1990 the final report was accepted by GBRMPA.

I enclose a set of indexed correspondence between the University, the Great Barrier Reef Marine Park Authority (GBRMPA), or other relevant departments and myself from prior to submission to the present and draw the Committee's special attention to the 1993 proposal and its background report. The remaining correspondence is relevant in that it details the events surrounding my employment under the UNIQUEST consultancy as well as my continued attempts to seek support for ideas central to the revision of the thesis. Although the examiners' comments were directed at my general failure to clearly state the thesis that was being defended, the thesis contained several unacceptable suggestions.

> "Juveniles of the common, sexually reproducing, large-bodied asteroids ..... were rare and the populations of these species were adult dominated throughout the study period " - page 41.
> "Considering the high reproductive effort displayed by most of the common species, there is little evidence of successful recruitment. It is possible, when the population is at low density, that many eggs are never fertilised " - page 49.

I suggest that much of the difficulty in obtaining supervision is related to the ideas that have been expressed in the thesis, 1986-1990 reports to GBRMPA and the 1993 proposal. In summary, I believe that most starfish eggs are not fertilised when starfish exist at non-outbreak density such as at Heron Island and an experiment to test this proposition formed the core of the 1993 extended project for which supervision was refused. The Crown of Thorns Starfish Research Committee (COTSREC) has invited resubmission of this proposal for consideration of funding at its next meeting in May 1994.

With respect to the decision before the Committee, although there is a preliminary question as to whether the suitability of any supervisor involves a question of law to be determined in accordance with the prescribed rules, my basic submission is that when the Academic Board gives a student the opportunity to revise and resubmit a thesis,

this opportunity is not conditional upon the obtaining of supervision. I believe that these matters have been the source of much confusion and require clarification. I thank-you for considering my requests and please let me know if I can be of any further assistance to the Committee in this matter.

.... End of submission

21 December 1993
POSTGRADUATE RESEARCH STUDIES COMMITTEE
UNIVERSITY OF QUEENSLAND, BRISBANE QLD 4072
Request for permission to resubmit a Doctor of Philosophy thesis without obtaining a supervisor.
JOHN CHARLES PATERSON (SN 687426-702) Applicant
SUMMARY OF ISSUES:

1. Is the suitability of a supervisor a question of law to be determined in accordance with the prescribed rules.
2. Is the opportunity to revise and resubmit a Doctor of Philosophy thesis conditional upon the obtaining of supervision.

Index to discussion documents

Document	Date	Pages
Request and Summary of Issues	21 Dec '93	1
Academic Record	1993	2
Letter from Zoology	9 Dec '93	3
Letter from Postgraduate Studies	30 Nov '93	4
Fax to GBRMPA	29 Nov '93	6
Letter to GBRMPA	26 Nov '93	7
Letter to Postgraduate Studies	23 Nov '93	8
Letter from GBRMPA	9 Nov '93	9
Letter from Postgraduate Studies	8 Nov '93	10
Letter from Zoology	24 Oct '93	11
Letter from GBRMPA	20 Sep '93	12
Letter to GBRMPA	17 Sep '93	13
Letter to GBRMPA	15 Sep '93	16
Letter to Zoology	26 Jul '93	17
1993 Proposal to Zoology	26 Jul '93	18
Background Report to Zoology	24 Apr '93	37
Letter from Zoology	10 May '93	41
Letter from DASSET	25 Mar '92	42
Submission to DASETT	14 Oct '91	45
Letter from Community Justice Program	13 Sep '91	46
Letter from Community Justice Program	27 Aug '91	47
Letter from Community Justice Program	26 Aug '91	48
Letter from Legal Aid Office	26 Jul '91	49
Submission to Legal Aid Office	24 Jun '91	50
Letter from Legal Aid Office	20 Jun '91	51
Final Report to GBRMPA	Jun '90	52
Letter from GBRMPA	31 May '90	95
Letter from GBRMPA	19 Mar '90	96
Report to GBRMPA	28 Feb '90	98
Consultancy Agreement	15 Jan '90	99
Letter from GBRMPA	12 Jan '90	102
Letter from GBRMPA	29 Nov '89	103
Letter from COTSARC	30 Mar '89	104
Letter from DASETT	17 Feb '89	105
Letter from GBRMPA	8 Feb '89	107
Letter from Australian Geographic	5 Jan '89	108
Letter from DASETT	23 Dec '88	109
Letter from GBRMPA	22 Dec '88	110
Media Release DASETT	21 Dec '88	112
Letter from Dalhold	6 Dec '88	113
Letter to Dalhold, etc	4 Dec '88	114
Letter to GBRMPA	2 Dec '88	115
Letter from GBRMPA	2 Dec '88	116
Letter to Minister of Environment	11 Nov '88	117
Letter from GBRMPA	24 Oct '88	120
Letter from GBRMPA	19 Aug '88	121
Advertisement GBRMPA	25 Jun '88	122
Letter from AIMS	18 Apr '88	124
Letter to Legal Officer	4 Mar '88	126
Letter from QDPI	25 Feb '88	127
Letter from AIMS	11 Feb '88	129
Letter from Nature	29 Jan '88	130
Letter from Dreamworld	28 Jan '88	131
Memorandum to Head Zoology	14 Jan '88	132
Letter to GBRMPA	11 Jan '88	133
Debtor Status Report	13 Oct '87	134

Letter to Student 4 Aug '87 135
Letter to Student (undelivered) 7 Jul '87 136
File note re letter undated 137
Note to Chair PGSC 6 Jul '87 138
Memorandum to Deputy Bursar 8 May '87 139
Minutes of P/G Studies Committee 2 Apr '87 140
Letter to Theses Section 31 Mar '87 142
Memorandum to Bursar 10 Mar '87 143
Letter to Student 5 Mar '87 144
Notice to Student 4 Mar '87 145
Letter to Student 10 Feb '87 146
Letter to Student 4 Feb '87 147
Statement by Dr Endean undated 148
Letter to Personnel Services 5 Jan '87 150
Letter to Student 5 Jan '87 151
Progress Report to GBRMPA 31 Dec '86 152
3 Monthly Report to Dr Endean 16 Dec '86 162
Letter to Student 5 Dec '86 170
Memorandum to Dr Endean 1 Sep '86 171
Letter to Registrar 4 Aug '86 172
Minutes of P/G Studies Committee 31 Jul '86 173
Letter to Reichelt 30 Jul '86 174
Offer of Appointment 22 Jul '86 175
Conditions of Appointment 1 Jan '85 176
Qualification for Appointment undated 178
Memorandum to Registrar 16 Jul '86 180
Letter to Student 7 Jul '86 181
Letter to Reichelt 1 Jul '86 182
Letter to Acting Head Zoology 27 Jun '86 183
UNIQUEST Consultancy Agreement 17 Jun '86 185
Memorandum to Head Zoology 17 Jun '86 197
Examiner's Report from Ebert 28 Mar '86 198
Examiner's Report from Yamaguchi 21 Mar '86 206
Examiner's Report from Reichelt 12 Feb '86 211
Statement by Supervisor 16 Dec '85 213
Memorandum to Deputy Bursar 31 Oct '85 214
Letter to Deputy Bursar 2 Oct '85 215
Letter to Student 2 Sep '85 216
Letter to Staff Officer 28 Aug '85 217
Letter to Registrar 27 May '85 218
Letter to Head Zoology 24 May '85 219
Supervisor's Report 20 May '85 220
Offer of Appointment 7 Nov '84 221
Letter from GBRMPA 16 May '84 222
Letter from GBRMPA 19 Jan '84 223
Letter from GBRMPA 8 Sep '82 224
Letter from GBRMPA 4 Sep '81 225

.... End of Request for permission

Background Report to PhD Proposal - Coral Reef Starfish

The crown of thorns starfish (Acanthaster planci) has stimulated much scientific research, and although many explanatory hypotheses have been proposed we do not understand why outbreaks of this starfish occur on some reefs while, on other nearby reefs, this starfish maintains a stable, low population density. The role of natural predators in maintaining high prey diversity, and the possible survival strategy of rarity in the coral reef community is unclear with respect to either starfish, their predators or their prey. The spatial distribution, population structure and fecundity of other starfish, while central to an understanding of these outbreaks, is not understood.

The PhD study sought answers to the following questions:

1. What starfish species are present at Heron Reef?
2. What is the spatial pattern of each species?
3. What is the population structure of each species?
4. What is the reproductive mode of each species?
5. Is the mean individual size stable for each species?
6. How diverse is this community?

Comparative data on these starfish might contribute usefully to an understanding of this outbreak phenomenon and with this broad aim in mind, the PhD study focused on Heron Reef which is a non-outbreaking reef at the southern end of the Great Barrier Reef. Factors that influence diversity and stability within the coral reef community should emerge when these results are compared with data from outbreaking reefs.

The thesis titled "Life-History Strategies of Coral Reef Asteroids" was submitted for the degree of Doctor of Philosophy at the University of Queensland on 5th December 1985. The central questions of the thesis were stated at the end of the introduction and the thesis to be defended was that on reefs where large-bodied starfish are uncommon they exist in a stable population structure with little recruitment.

The thesis also suggested that:

(1) there was little competition between starfish,
(2) the starfish represented a recruitment-limited species assemblage,
(3) high specificity at settlement was necessary for the survival of post-settlement juveniles, and
(4) the ability to disperse widely was necessary for the survival of many starfish species.

These propositions were consistent with the low density and patchy starfish distribution at Heron Reef but were clearly not conclusions

derived logically from established facts. Both external examiners incorrectly believed that these suggestions were the thesis that was being defended.

The student's research had been supervised by Dr Endean of the Zoology Department. Although Dr Endean agreed that the thesis was in an appropriate form for submission, he commented on the submission of the thesis that "much more could have been made of the information obtained. For example, the candidate has failed to give adequate attention to the theoretical implications of the principal findings made". Dr Endean stated further following the return of the examiner's reports that "It is my belief that no additional field work by the candidate would be required as adequate data are available for a meaningful revision which would take into account the cogent comments made by all referees."

The extracts of the examiners' reports which were forwarded to the Head of Department, Dr Endean and the student did not include Dr Yamaguchi's comment that "there are considerable amount of data which should be treated more carefully and they would be strengthened by collecting additional information, so that the candidate should be encouraged to complete this work to be acceptable for the degree". In addition, Prof Ebert stated that "The data do not directly address important problems of competition, recruitment or dispersal. What this means, I am suggesting, is that the thesis to be defended must be recast OR that additional data must be presented that address the defence of the thesis as it is stated".

The student had tutored in the Zoology Department for several years and under the conditions of appointment for tutorial staff approved by University Senate, no further tutorial appointment was possible beyond 1985. The student was ineligible for Tertiary Assistance and was required to pay student charges from which he had been exempt whilst employed as a tutor. Prior to the student's notification that he was required to revise and resubmit his thesis within 12 months, he was employed full-time by Queensland University under a consultancy agreement between the Great Barrier Reef Marine Park Authority and UniQuest Ltd signed on 17-June-1986.

The Consultancy Agreement specified that a Research Fellow (at least 6 years post-doctoral experience) and a Research Assistant be appointed to undertake the work. Although the University knew that the student was required to revise and resubmit his thesis within 12 months and although the student's contract of employment was not finalized until 4-August-1986, the student commenced employment

with the University on 26-June-1986 as a Research Officer. The student was advised that his thesis had not been approved on 7-July-1986 while the University had been aware of this fact since 17-June-1986.

The Consultancy Agreement contained a clause which provided that "The Consultant, its employees or agents shall not disclose or make public any information or material acquired or produced in connection with or by the performance of the services without prior approval in writing of the Authority".

Dr Endean was one of the three Principal Investigators involved in the Consultancy which provided for the "study of crown of thorns starfish predators on or in the vicinity of reefs of the Great Barrier Reef". Project execution involved "searching in areas of crown of thorns starfish aggregations for predators and instances of predation" as well as "enclosure and possibly aquarium studies of potential predators". This student and another worked in the field.

The Giant Triton (Charonia tritonis) is a well-known but rarely encountered predator of many species of starfish on the Great Barrier Reef. It was the only observed predator of adult starfish throughout the entire period of the students' employment under the Consultancy Agreement. Both students believed that the triton was a voracious predator of starfish and that it occurred with a frequency much greater in regions of residual crown of thorns starfish outbreak than had been observed at Heron Reef.

At John Brewer Reef, the triton's aggregated spatial pattern and prey preference seemed sufficient to account for the observed reduction in adult crown of thorns starfish numbers within the area of residual starfish outbreak. If a similar sized but dispersed population of tritons occurred at Heron Reef, it could easily have remained undetected but still be sufficient to explain the low abundance of starfish on that reef. John Brewer Reef was the only readily accessible reef that contained a residual population of crown of thorns starfish and the isolation of triton aggregations was a condition precedent to the establishment of a general triton census technique.

Both students asserted that the triton was predominantly cryptic, and that density estimates which were based on snorkel swims or manta surveys, rather than detailed scuba searches by skilled observers, would grossly underestimate the triton's abundance and in particular fail to establish whether the triton aggregated in the vicinity of crown of thorns starfish aggregations. The establishment of this fact was relevant to the revision of the student's thesis and to any survey

technique agreement between UniQuest and the Authority because it was relevant to the expected correlation between starfish numbers and predator numbers.

While a large-scaled negative correlation between starfish and predator abundance is predicted by the Predator Control Hypothesis, a medium-scale positive correlation will be predicted if predators aggregate in areas of prey aggregation. The observation of prey dispersion following unsuccessful predator attack and a further negative correlation between starfish and predator abundance on an even finer scale was proposed. This latter proposition and the implication of reduced starfish egg fertilization in dispersed starfish aggregations was raised by both students. There was great potential for confounded variables unless the degree of predator aggregation was determined prior to the establishment of a general predator census technique.

These matters were a source of major contention between the students and Dr Endean and resulted in both students' dismissal. All the relevant facts as well as any implications that were relevant to the execution of the Consultancy Agreement or might be relevant to the revision of the thesis were communicated to both Dr Endean and the Authority. There was a great conflict of interest between Dr Endean's role as PhD supervisor and his role as a Principal Investigator under the Consultancy Agreement. The Authority was aware of this conflict of interest.

In a letter addressed to Theses Section 31-March-1987 the student requested an extension of time for submission as well as an exemption from administrative fees to allow resubmission. This letter was stamped by Records Section on 7-April-1987 but no reply was received by the student and he assumed that an extension of time for resubmission and the granting of fee exemption had not been immediately approved. Under a recent Freedom of Information request the student discovered that the University's response had been greatly delayed and consequently was not delivered to the student.

When the students' employment was terminated by the University the students were overpaid due to an error on the part of the University. The University initiated legal proceedings to recover this overpayment even though it was a direct and foreseeable consequence of the University's own negligence. It was only when the University received legal advice that the students were likely to succeed in their countersuit that the legal proceedings were dropped by the University. As a consequence of this litigation any possibility of a reconciliation

between the students and Dr Endean was impossible. The student believes that this animosity still continues. Dr Endean has now retired.

The student notified the University that he wished to revise and resubmit his thesis and the letter of 31-Mar-1987 is prima facie evidence of this fact. There has been a considerable delay in applying for reenrolment and the student agrees that the nature of the revision could be quite extensive but is prepared to give full consideration to all cogent comments. With respect to the delay in reenrolment, the student submits that it is relevant that the University maintained contact with him throughout the extensive period of litigation but did not respond to his letter of 31-Mar-1987 regarding revision of his thesis. An equitable remedy is being sought that includes a supervised project incorporating much of the previous work.

The student will comply with the conditions expressed in the University's undelivered letter of 7-July-1987 regarding reenrolment and any further requirements of the Post-Graduate Studies Committee. The student knows that it is necessary to obtain a new supervisor before the nature of the revision can be finalised. The student is presently seeking a supervisor for the project and will advise when he has found supervision that complies with the PhD rule requirements.

J.C.Paterson - Semester 1, 1993.

.... End of Background Report

Thesis Defense:

With respect to the specific points raised by Dr Yamaguchi in his examiners report, the candidate is unclear as to whether Dr Yamaguchi's words "may be considered" conveys the intention "should or shall be considered" with respect to revision of the thesis. All of the substantial matters raised by Dr Yamaguchi were considered by the candidate but perhaps they have been given lesser consideration than Dr Yamaguchi would wish.

The candidate wishes to address the specific points raised by Dr Yamaguchi with the purpose of clarifying the issues involved and isolating relevant criticisms from what may merely be differing personal sentiments. Before addressing these numbered points systematically, the candidate wishes to draw the Committee's attention to the opening lines of Dr Yamaguchi's detailed report:

"This thesis is largely descriptive with many speculations not supported by observations or established ideas ... there is almost no new information which may contribute to the advancement of scientific thought".

It is possible that Dr Yamaguchi has identified with a philosophy and been offended by views expressed by the candidate in the introduction of the thesis. The candidate would wish to clarify that the philosophic matters were not directed specifically at Dr Yamaguchi and would wish to leave personal sentiments out of the examination process and to concentrate on science.

1. Regarding "community" and "species assemblage".
The candidate agrees with Dr Yamaguchi that the term "species assemblage" is the correct term for the set of species within a certain taxa that occur at a locality such as Heron Reef. However, while the candidate's failure to adequately distinguish between the set of coral reef asteroids found at Heron Reef and the set of taxa which constitute the coral reef is a potential source of confusion when the word "community" is used for both sets, the meaning should to some extent be conveyed by the context in which the word was used in the discussion and the candidate fails to understand why Dr Yamaguchi was unable to make any sense whatsoever out of the discussion at the conclusion of chapter 11. The candidate feels that it will be necessary to distinguish further the set of coral reef asteroid species which have ever been located anywhere within the tropical Indo-West Pacific region as this set has also been referred to as the "coral reef asteroid community" in this and other chapters of the thesis.

2. Regarding feeding habits and food qualities.
The candidate wishes to clarify that the feeding habits of "felt-feeding" asteroids were observed in the field with the purpose of establishing a prey preference for conspicuous reef organisms whose patterns of abundance might either effect or reflect asteroid abundance. It was beyond the scope of this study to undertake deep investigations of microscopic food quality and this was clearly stated in the relevant chapter on diet and microhabitat.

The candidate maintains that the paradigm of "resource limitation" is virtually infinite being not limited merely to food resources but potentially including any necessary ecological requirement. With respect to the recruitment of these asteroids, the candidate suggested that there may be specific sites at which the survival of post-settlement stages is enhanced and would submit that discussion of such matters is not precluded by either the absence of detailed data on food partitioning or by the absence of conclusive results with respect to inter-specific competition.

The candidate submits that whether or not food partitioning or inter-specific competition occurs is a question of fact and irrespective of the depth of investigation this fact may or may not be established correctly. The candidate submits that the question of whether alternate explanations are consistent with the available evidence is a question of law and the distinction must always be made between finding the facts and deciding the law. It is a foundation principle of both modern science and law that discussion of alternative explanations cannot be limited arbitrarily without the due process being misdirected. Such matters were stressed in the introduction of the thesis.

3. Regarding the thesis to be defended.
The candidate agrees with Dr Yamaguchi that the frequency of feeding activities, nutritional value of the felt, size and type of stomach are all very important in relation to energy budgets but this was never one of the main points in the thesis. The aims of the research were outlined at the conclusion of the introductory chapter but there still seems to be a general misunderstanding of the thesis that was being defended. The major findings are that some species existed in stable size and abundance structures and that some areas on Heron Reef had low numbers of starfish compared with others. The thesis to be defended was that on reefs where large-bodied starfish are uncommon they exist in a stable population structure with little recruitment. To place the data collection and analysis in perspective, it must be remembered that the large scale of sampling was determined by the relatively low

abundance of starfish at Heron Reef compared to outbreaking reefs.

The candidate wishes to stress that a number of propositions were advanced in discussion as explanations of the available evidence. The proposition that there may be specific sites for better survival of post-settlement juveniles was never an assumption from which the lack of recruitment to the adult dominated populations was concluded. On the contrary, it is submitted that the case for lack of recruitment is sustained by empiric support not by logical conclusion. The proposition was one of fact which may or may not be true, but it was not the thesis that was being defended.

.... End of Thesis Defense

In 1994, Dr Endean was brought out of retirement to supervise the resubmission, and a revised thesis was resubmitted in 1995 and the degree of Doctor of Philosophy was awarded by the University of Queensland the following year.

In 2001, the following answers to questions on notice were provided by Ms Virginia Chadwick, the Chairman of the GBRMPA. The following comment summarizes the feeling of the GBRMPA regarding the role of the giant triton:
“All research associated with the Crown-of-thorns starfish phenomenon is currently being reviewed by the Cooperative Research Centre for the Great Barrier Reef World Heritage Area. Any further research on the giant triton will be subject to the findings of this review. However, given the theoretical and quantitative problems with the predator removal hypothesis, and the lack of scientific evidence to support this theory, it is likely that other avenues of research into the Crown-of-thorns starfish will be of higher priority.”

Questions to Senate Estimates Committee by Senator Nick Bolkus re: giant triton

Environment, Communications, Information Technology and the Arts Legislation Committee
Additional Information Received
VOLUME 2, ENVIRONMENT AND HERITAGE, PORTFOLIO
21 February 2001

Additional Information Relating to the Examination of Proposed Additional Expenditure for 2000-2001, Outcome 1,
Environment Question No. 49
Division: Great Barrier Reef Marine Park Authority, Topic:
Giant Triton Shell
Written question on notice: Tabled
1. Senator Bolkus asked:
Is the giant triton a natural predator of the Crown-of-thorns starfish?
Answer:
Yes, several studies have indicated that the giant triton does prey upon crown-of-thorns starfish (COTS).
2. Senator Bolkus asked:
Is the giant triton protected in Queensland?
Answer:
In 1969, the Queensland government introduced a ban on the collecting of giant triton. The Regulations to the Qld Fisheries Act, 1994 lists the giant triton in Schedule 4, Part 3, Division 5, as a fish regulated by species and thus is not to be collected. Within the confines of the Great Barrier Reef Marine Park, the giant triton is referred to as a protected species in Schedule 3 to the Regulations of the Great barrier Reef Marine Park Act 1975. In the Far Northern, Cairns and Mackay/Capricorn sections of the GBRMP the regulations state that: "an organism included in Schedule 3 is not to be collected, except by a traditional inhabitant, within the meaning of the zoning plan, for his or her own use."
3. Senator Bolkus asked:
Is the giant triton protected internationally?
Answer:
The UNEP World Conservation Monitoring Centre database reveals that the giant triton is not listed as a threatened or endangered animal, nor is it listed on the IUCN Red lists or on Convention on International Trade in Endangered Species (CITES) lists. However, Australia did support a proposal to list this species on CITES in October 2000.
Nevertheless, protection of the giant triton internationally currently depends on the management initiatives of the individual countries

where giant triton are found. For example, the giant triton is protected in some Pacific countries such as Fiji.

4. Senator Bolkus asked:

Are giant tritons for sale in Australian shell shops?

Answer:

Yes, giant triton shells can be purchased in Australian shell shops

5. Senator Bolkus asked:

How much do they usually sell for?

Answer:

The retail prices for giant triton shell varies between $20-$200 depending on the size and condition of the shell.

6. Senator Bolkus asked:

Would these giant tritons have been collected live from coral reefs?

Answer:

Most probably.

7. Senator Bolkus asked:

Would these giant tritons have come from outside Australia?

Answer:

Most probably.

8. Senator Bolkus asked:

How do we know that these giant tritons don't come from the Great Barrier Reef?

Answer:

There is no way to determine if a triton shell for sale was collected from the Great Barrier Reef or overseas

9. Senator Bolkus asked:

What do we know of the present abundance of the giant triton on the GBR?

Answer:

Very little is known about the present abundance of giant triton on the GBR. However, the triton is considered by some as rare. Surveys conducted by Endean of over 130 reefs between 1966 and 1972 showed only 78 tritons. Nevertheless, the triton is a cryptic and nocturnal animal. Coral reefs provide many hiding places for cryptic animals and this complicates efforts to accurately assess their numbers. The nocturnal habits of the giant triton make them even more difficult to locate and accurately count in the reef environment.

10. Senator Bolkus asked:

What do we know of the past abundance of the giant triton on the GBR?

Answer:

The is no scientific survey information available before the 1960's to indicate what the natural abundance of tritons would have been on the GBR. However, the Qld Fisheries Service advised the Hon. Rod Welford

in October 2000 that records do not indicate a large amount of commercial collection as they are a cryptic and naturally non-abundant species.

11. Senator Bolkus asked:

Do we know how many of these giant tritons were collected in the past?

Answer:

There are few records pertaining to the collection of giant triton. However, it is known that indigenous people have traditionally harvested triton, and it is also known that since the 1930's, giant triton have been harvested by shell collectors and until about 1960, they were also collected by the crews of fishing luggers involved in the trochus trade. Nevertheless, with a dozen of these luggers operating at any one time, Endean estimated that these crews collected about 10,000 triton per year and there is anecdotal evidence that triton were very abundant prior to collecting.

12. Senator Bolkus asked:

Has the collection of giant triton shells reduced their population numbers?

Answer:

Because there are no historical records for the numbers of triton naturally occurring on the Great Barrier Reef, there is no way to accurately determine whether collection of giant triton shells for sale between 1930 and 1960 has caused a decline in their population. However anecdotal evidence is that collection of giant triton has reduced their numbers.

13. Senator Bolkus asked:

When was this predator of the crown-of-thorns starfish discovered?

Answer:

The first scientific studies to indicate that the giant triton is a predator of crown-of-thorns starfish was published in 1969.

14. Senator Bolkus asked:

Do we know for sure what is the feeding rate of the giant triton?

Answer:

Research by scientists such as Chesher, Pearson and Endean in the late 60's has shown that tritons consume crown-of-thorns starfish at a relatively slow rate, as slow as 0.7 starfish per triton per week. Furthermore, research by Chesher in Micronesia has demonstrated that these attacks are not always successful and that the starfish may often escape and regenerate any damaged tissue or limbs.

15. Senator Bolkus asked:

Do we know for sure what is the prey preference of the giant triton?

Answer:

Research conducted in the late 60's by scientists such as Chesher,

Pearson and Endean indicates that although giant triton do consume COTS, they prefer other species and should be considered as a generalised predator that feeds on a variety of starfish and holothurians. To quote Potts 1981: "Indeed, A. planci (the Crown-of-thorns starfish) seems to be very low in the triton's hierarchy of food preferences."

16. Senator Bolkus asked:

What research has been undertaken on the ecology of the giant triton?

Answer:

Research into the feeding preferences and feeding habits of the giant triton were conducted in the late 60's, and triton were counted at reefs where COTS outbreaks were taking place. Other than that I am not aware of any field based studies of giant triton ecology. As cryptic and nocturnal animal, field studies into the giant triton's ecology are difficult to conduct. To quote Engelhardt and Lassig 1996, "The identified lack of information on key parameters combined with an inability to obtain sufficient numbers of c. tritonis for quantitative studies remains the main obstacle in improving our understanding of its role as a natural predator of a planci."

17. Senator Bolkus asked:

What abundance of giant triton would it take to keep starfish rare?

Answer:

Widely accepted scientific opinion is that giant triton are unable to keep the Crown of thorns starfish rare, no matter what their abundance. There is no scientific evidence to suggest that predation by the giant triton could either prevent or control COTS outbreaks. At the height of an outbreak, a single reef may harbour up to 2 million starfish, as reported by Cameron and Endean on Green Island in 1981. Given the slow feeding rate (0.7 starfish per week) and the fact that attacks on COTS by tritons are not always fatal, the ability of tritons to control or prevent COTS outbreaks is doubtful. To quote Chesher 1969: "My studies indicate that predation by C. tritonis would not result in adequate controls of A. planci populations. " and "even if triton were abundant, it would be doubtful that it could control A. planci.". Furthermore, scientists such as Endean, Chesher, and Ormond have recorded COTS outbreaks on reefs in Micronesia and the Red Sea where tritons are relatively abundant (Potts, 1981).

A review of COTS research by Potts in 1981 and later by Moran in 1988, reinforces these views. Potts notes that of all the hypothesis to explain COTS outbreaks, the predator removal hypothesis (that is, removal of predators such as the giant triton) was "the least satisfactory on both theoretical and empirical grounds" and Moran states that "there are little direct, quantitative data to suggest that predation plays an

important role in limiting the numbers of starfish on reefs."
18. Senator Bolkus asked:
What research has been undertaken on breeding the giant triton?
Answer:
I am not aware of any research programs that investigated breeding of the giant triton at this time.
19. Senator Bolkus asked:
What is the future of the Giant Triton Research program?
Answer:
All research associated with the Crown-of-thorns starfish phenomenon is currently being reviewed by the Cooperative Research Centre for the Great Barrier Reef World Heritage Area. Any further research on the giant triton will be subject to the findings of this review. However, given the theoretical and quantitative problems with the predator removal hypothesis, and the lack of scientific evidence to support this theory, it is likely that other avenues of research into the Crown-of-thorns starfish will be of higher priority.
…. End of Questions to Senate Estimates Committee
In mid-2001, further surveys of the giant triton were conducted on Beaver Reef, off Mission Beach. The tourist operator, Quick Cat Cruises was conducting a starfish control program and these surveys were conducted in the vicinity of starfish control. A number of giant tritons were located, and their feeding and movements were studied. In 2002, a video of the giant triton attacking and consuming crown-of-thorns and other starfish was produced and shown to Dean Wells, the Queensland Minister for the Environment. This video was subsequently uploaded to YouTube. This project was discontinued later that year when the experimental animals were released and not able to be tagged with ultrasonic transducers due to lack of funding.

In 2014, Dr Mike Hall of the Australian Institute of Marine Science (AIMS) lead a research team investigating the giant triton. In 2017, AIMS implemented the Giant Triton Sea Snail Breeding Program which continued to 2019. Like similar research conducted by Japan, Thailand and Korea, while many planktonic larva were produced, they would not settle as benthic juvenile shells.

How a Crown-of-Thorns starfish reacts to the smell of a Giant Triton – AIMS research